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BIOLOGY,
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ND CONTROL OF
Aedes albopictus

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BIOLOGY, DISEASE RELATIONSHIPS, AND CONTROL OF *Aedes albopictus*

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PREFACE

The first version of this document, titled "Ecology, Biology, and Control of *Aedes albopictus* (Skuse)," was prepared in January 1987 to provide scientific and technical background for the "Plan of Action on *Aedes albopictus* in the Americas." It was discussed at the 99th Meeting of the Executive Committee of the Pan American Health Organization (PAHO), held in Washington, D.C., in June 1987 (PAHO Document CE99/15, 1987). The document was produced by the Communicable Diseases Program under the coordination of Dr. F. J. López-Antuñano and was a joint effort of Dr. José G. Estrada-Franco, PAHO Temporary Adviser; Dr. George B. Craig, Biology Department, University of Notre Dame; and Drs. Francisco Pinheiro, Bruce Knudsen, and Michael Nelson of PAHO/WHO. Since the 1987 version was produced, three excellent reviews on the biology, genetics, and disease relationships of *Aedes albopictus* have appeared, in addition to a plethora of scientific articles on the species (Hawley, 1988; Rai, 1991; Mitchell, 1991).

This second version is presented in order to include important information about this mosquito species that has been brought to light during the past five years by a series of studies and research projects conducted primarily in the United States of America. The findings of these studies provide some insight into what could become one of the important arthropod vectors of human diseases and zoonoses in the American Region. This document is published in the hope that it will be of value to health agencies in the Americas that are concerned with vector surveillance and control.

INTRODUCTION

Until the early 1980s *Aedes albopictus* was assumed to solely inhabit certain islands of the Indian Ocean, various countries in the oriental region of Asia, and the Hawaiian Islands in the Pacific Ocean (Huang, 1972). In the mid-1980s, however, this picture underwent a sudden and alarming shift.

In August 1985 *Ae. albopictus* mosquitoes were discovered breeding in tire dumps in Harris County, in and around Houston, Texas. The Houston *Ae. albopictus* population represented the first established infestation reported in the Western Hemisphere (Centers for Disease Control and Prevention [CDC], 1986a; Monath, 1986; Sprenger and Wuithiranyagool, 1986). To date, *Ae. albopictus* has been reported from 22 other states in the United States of America as it has moved northward, the northernmost point thus far being Chicago, located at about 42° latitude (D. Gubler, pers. comm., 1993). The southward movement of *Ae. albopictus* in the United States has reached the city of Brownsville, Texas, located at 25°54.3′ latitude (Womack, 1993).

Elsewhere in the Americas, *Ae. albopictus* was first reported in Brazil in June 1986 in the states of Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo (Forattini, 1986; Parigot, 1986). By April 1994 the species had been reported in three more states—Maranhão (San Luis de Maranhão) and Bahia and Paraná (several locations)—for a total of 673 infested municipalities (J. C. Mangabeira da Silva, pers. comm., 1994). The extent of Brazil's *Ae. albopictus* infestation prompted a panel of experts, meeting at PAHO Headquarters in 1986, to hypothesize that the species was first introduced into the country some years ago (PAHO, 1987; CDC, 1986b).

Furthermore, the third and fourth countries with established infestations have recently been identified: the Dominican Republic, where the mosquitoes have been found mainly in parkland areas of the capital city of Santo Domingo (C. Peña, National Malaria Program, pers. comm., June 1993), and Mexico, with infestations in towns along the U.S.–Mexico border in the states of Coahuila and Tamaulipas (C. Castañeda-Barrón, Tamaulipas State Health Services, pers. comm., 1992; C. Moore, pers. comm., 1993). The species has also been reported in continental Africa and Europe (Savage et al., 1992; Sabatani et al., 1990).

The potential threat posed by the presence in the Americas of this exotic and efficient vector species of dengue and possibly yellow fever and other arboviruses has generated great concern among the countries (PAHO, 1987).

The intent of this document is to bring together the information available to date on the biology, disease relationships, and control of *Ae. albopictus*. The Asian information, summarized in our 1987 document, is supplemented by the findings of studies conducted mainly in the United States, with emphasis on data generated in the 1990s.

PHYLOGENETIC RELATIONSHIPS AND GEOGRAPHICAL DISTRIBUTION

Aedes albopictus was first described by Skuse in 1894 from specimens collected in the city of Calcutta on the Indian subcontinent (Barraud, 1928). Phylogenetically, the species has been placed in the order Diptera, suborder Nematocera, family Culicidae, genus *Aedes*, subgenus *Stegomyia*, group *scutellaris*, and subgroup *albopictus* (Huang, 1972; Rai et al., 1982).

It is believed that *Ae. albopictus* originated in the tropical forest of Southeast Asia, where many closely related species are known to coexist (Smith, 1956). This area is also considered to be the place where classical dengue had its origin. Another medically important *Stegomyia*, *Aedes aegypti*, is thought to have been introduced into Asia from Africa (Mattingly, 1957). These two species are the most important vectors of dengue in Southeast Asia (Smith, 1956; Pant et al., 1973; Chan, 1985). In Asia, *Ae. albopictus* occurs as far north as Beijing, China, at 40° latitude (World Health Organization [WHO], 1980). It is also distributed in the Korean peninsula and in Japan to northern Honshu, Japan's main island, reaching the city of Sendai at 36° N (Kamimura, 1968; Hong et al., 1971). Beijing and Chicago, Illinois (at about 42° north latitude in the United States), are the northernmost reported distribution points of *Ae. albopictus* in the Palearctic and Nearctic regions, respectively.

In Southeast Asia the species has extended its range to the coastal cities of Irian Jaya, the Solomon and Santa Cruz Islands, and Papua New Guinea; it has also been found in Brisbane and Darwin, Australia, where the infestations were promptly eradicated (Elliot, 1980; D. Gubler, pers. comm., 1993), and recently in New Zealand (Kay et al., 1990; Craig, 1993). It has been reported in the Mariana, Caroline, and Hawaiian Islands, Palau, the Asian continent, and westward to several islands in the Indian Ocean such as Madagascar, Mauritius, Reunion, the Seychelles, and the Chagos Archipelago (Surtees, 1966; Lambrecht and Van Someren, 1971; Ho et al., 1972). In addition, the species

has recently been found in Europe (Albania and Italy) and in mainland Africa (coastal South Africa and various villages in Nigeria) (Sabatani et al., 1990; Savage et al., 1992; Craig, 1993; see references in Hanson and Craig, 1994). Also, as noted above, *Aedes albopictus* has recently colonized portions of four countries of the Americas. It has been found in midwestern and southern states in the United States, three towns in northern Mexico along the border with Texas, seven states in Brazil, and parts of the city of Santo Domingo in the Dominican Republic (Moore et al., 1988; Mangabeira da Silva, pers. comm., 1994; Moore, pers. comm., 1994). The species is now known to occur on all continents except Australia and Antarctica. Map 1 summarizes the worldwide distribution of *Ae. albopictus*. Maps 2 and 3 illustrate its distribution in three countries of the Americas.

In terms of altitude, *Aedes albopictus* has been found up to 1,800 meters in the mountains of Thailand (Scanlon and Esah, 1965). Pant and co-workers (1973) reported the presence of *Ae. albopictus* in a Thai village located at 1,700 meters. Both studies noted finding the species at every altitude surveyed, from sea level to the highest. Ho et al. (1972) reported maximum altitudes for *Ae. albopictus* of 24 to 180 meters in West Pakistan, Sri Lanka, Taiwan, and Malaya, but this study appears to underestimate the mosquito's vertical range. In the United States the highest altitude reported for the species is 305 meters at New Alsace, Indiana (Focks et al., 1994).

One of the most important differences between the North American populations of *Ae. albopictus* and *Ae. aegypti* is their latitudinal distribution. While *Ae. aegypti* populations are limited to the southern portions of the United States due mainly to their inability to tolerate very low temperatures, *Ae. albopictus* populations have evolved a photoperiod-induced egg diapause, which allows them to colonize temperate and northern latitudes. In addition, temperate strains of *Ae. albopictus*, such as the North American ones, show egg cold hardiness, which enables the species to survive the suboptimal winter temperatures found in the northern latitudes (Hawley, 1988).

While the distribution of *Aedes albopictus* and that of *Aedes aegypti* can overlap in the same urban environment (Harrison et al., 1972; Azzizar, 1980; Chan, 1985), *Ae. albopictus* is more commonly found in suburban and rural areas where open, vegetated spaces are prevalent (Ho et al., 1972; Pant et al., 1973; Chan, 1985). It is generally accepted that *Ae. albopictus* was originally a sylvan species, breeding and feeding in forest fringes, which began to adapt to the domestic environment throughout several parts of its geographical range (Bonnet and Worchester, 1946; La Casse and Yamaguti, 1950; Surtees, 1970; Miyagi et al., 1983). In the United States, studies based on ovitrap collections carried out in New Orleans, Louisiana, in 1987 showed that *Ae. albopictus* was the most abundant species in suburban environments. These habitats are characterized by open areas with plentiful vegetation, surrounded by buildings. By contrast, in more urbanized sections of the city, *Ae. aegypti* appears to remain the dominant species (New Orleans Mosquito Control Board [NOMCB],[1] 1987). The tendency of *Ae. albopictus* to inhabit natural containers (tree holes and bromeliads) in places where vegetation is abundant has also been observed in several other areas of the United States and Brazil (O'Meara et al., 1992; Gomes et al., 1992). As in Asia, American *Ae. albopictus* have shown a much greater propensity for using natural containers than have *Ae. aegypti*.

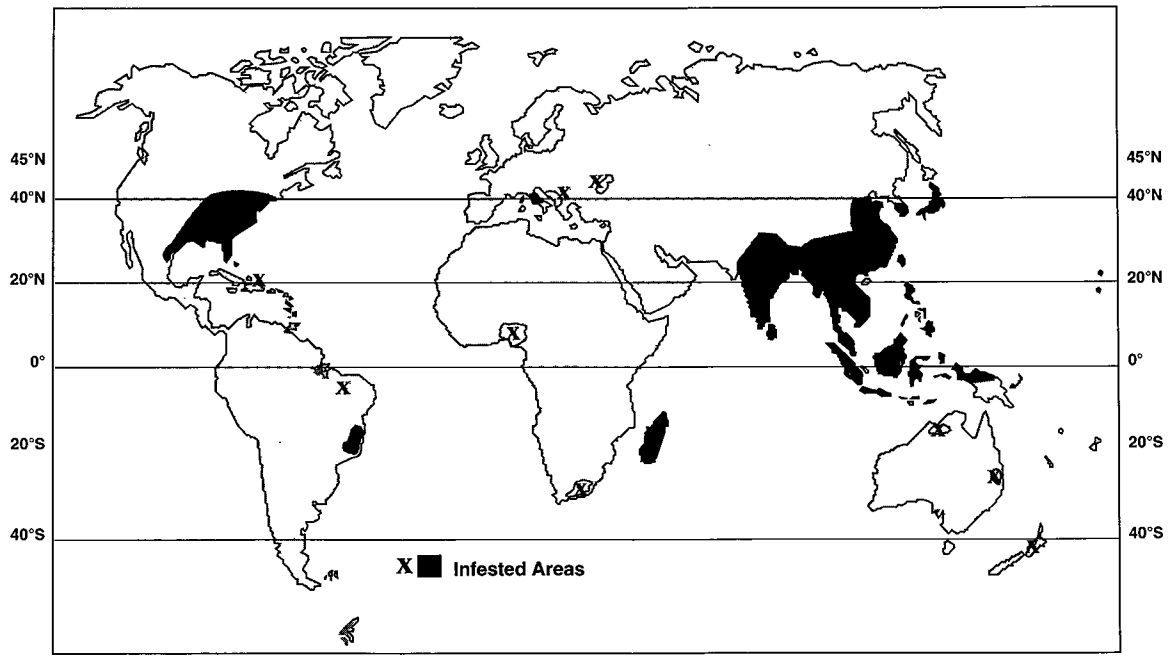
BIOLOGY

In the United States, the duration of the larva-to-adult phase of the life cycle of *Ae. albopictus* in tires was estimated by comparing the population density of early instar larvae with that of emerging adults. Studies conducted during the spring of 1989 in New Orleans (average ambient temperature of about 26 °C) with field populations of *Ae. albopictus* established that the average time period between a peak abundance of first instar larvae and a peak abundance of emerging adults was about 10 days (NOMCB, 1989). Under natural conditions in Viet Nam, eggs of *Ae. albopictus* have been reported to reach adulthood in 7–20 days in spring and 24 days in winter (Surtees, 1966; Ho et al., 1972). Under laboratory conditions, studies that assessed the effect of environmental parameters such as temperature and other variables produced similar results, as reported by different authors.

Matsuzawa and Kitahara (1966) found that for *Ae. albopictus* the interval from the moment of oviposition to emergence of the adult stage lasted 12, 13.7, and 24.3 days at water temperatures of 30 °C, 25 °C, and 20 °C, respectively. Hien (1975a) reported development times from oviposition to emergence of 11 days at 30 °C, 14 days at 25 °C, and 23 days at 20 °C. Galliard and Golvan (1957), working with a laboratory-reared strain of *Ae. albopictus*, found that development from egg to adult took 25 days and 10 days at 18 °C and 25 °C, respectively. Livingstone and Krishnamoorthy (1982) determined that at room temperature (26 °C to 30 °C) development from egg to adult of female *Ae. albopictus* ranged from 11 to 12.4 days, whereas males reached the adult stage in 10 to 11.4 days. The optimal water temperature for *Ae. albopictus* development has been reported to be 25 °C. At this temperature the egg incubation period is two days (Sheng and Wu, 1951; Ho et al., 1972).

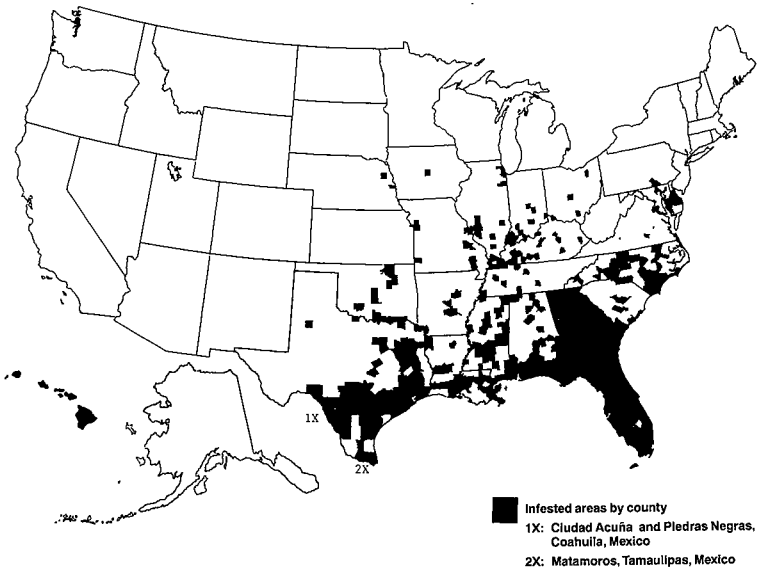
In addition to temperature, food supply also affects the size and development time of the *Ae. albopictus* larvae. Larvae placed in contaminated water with high organic content were found to develop rapidly, while starvation and

[1]Address: 6601 Lakeshore Drive, New Orleans, LA 70126.



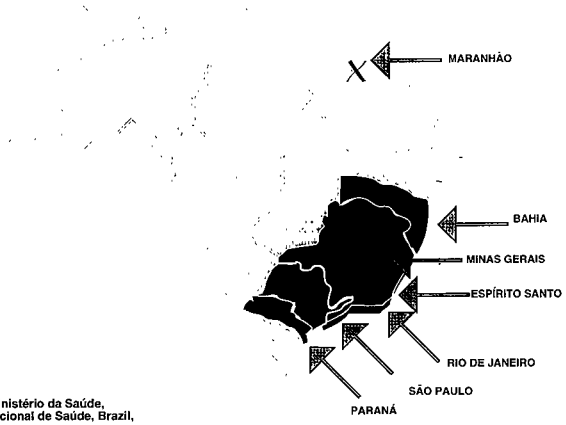
Sources: Hong et al., 1971; Kamimura, 1968; Huang, 1972; Elliot, 1980; C. Moore, pers. comm., 1993; J.C. Mangabeira da Silva, pers. comm., 1994.

Map 1. ***Aedes albopictus*** **distribution documented in the world as of April 1994**



Data from: Dr. Chester Moore, Division of Vector-Borne Infectious Diseases, Centers for Disease Control and Prevention, Fort Collins, Colorado; C. Castañedo-Barrón, Tamaulipas State Health Services, and S. Ibáñez-Bernal.

Map 2. ***Aedes albopictus*-infested areas in the United States of America and northern Mexico, as of December 1994**



Data from: Ministério da Saúde, Fundação Nacional de Saúde, Brazil, 1994.

Map 3. ***Aedes albopictus*-infested areas in Brazil, by state, April 1994**

overcrowding retarded development and increased mortality under laboratory and field conditions (Mori, 1979). In general, the duration of the larval stage was extended by decreasing the food supply and shortened by increasing it. At 0.035 mg food/larva/ml, the mean development time from egg hatching to adult was 6.1 days, while at 0.004 mg/larva/ml, the duration was 32.4 days (Chan, 1971).

Variables known to affect the life cycle of any mosquito species include food, photoperiod, relative humidity, and temperature. Significant information on how these factors affect each developmental stage is summarized below.

Eggs

Mosquito eggs (including those of *Aedes* spp.) are not fertilized until the moment before they are actually laid. Sperm stored in the spermatheca enters each fully developed egg (oocyte) as it passes the opening of the spermathecal duct on its way out. Once the eggs have been laid, karyogamy occurs and development of the embryos proceeds. Embryonic development may be defined as the developmental changes taking place in the egg between fertilization and hatching (Christophers, 1960). The length of the period of embryonic development depends mainly on the temperature and relative humidity to which the eggs are exposed.

Laboratory observations have shown that Asian strains of *Ae. albopictus* eggs embryonated in periods of two to four days at temperatures between 24 °C and 27 °C (references in Hawley, 1988). Ideal conditions for embryogenesis of *Ae. albopictus* eggs from the Americas appear to be exposure under natural and laboratory conditions to a temperature of 21 °C, a relative humidity of 70%–80%, and a photoperiod of 16L:8D hours for six to seven days (NOMCB, 1989; Edgerly et al., 1993; Hanson and Craig, 1994). Once embryogenesis has been completed, the eggs can stay unsubmerged and almost completely dry for long periods without loss of viability.

Egg survival may depend on a combination of density-dependent and density-independent selective pressures. Events that may promote egg loss include desiccation, predation, and freezing. Egg survival also may be affected by certain female parental factors such as unembryonated eggs that collapse or eggs that fall off because they are not properly attached to a substrate. We will focus on such factors as desiccation, predation, and freezing, since to the best of our knowledge no studies have dealt with the female parental effects on *Ae. albopictus* egg survival.

Ae. albopictus eggs survive desiccation in a wide variety of indoor and outdoor artificial containers (flower pots, earthenware jars, tin cans, coconut shells, tree holes, bamboo stumps, etc.) and hatch as soon as the containers fill up with water (Feng, 1937; Ho et al., 1972). The number of *Ae. albopictus* eggs that survive low humidity appears to depend upon the development stage of the embryos before they are exposed to dry conditions. Gubler (1970a) found that *Ae. albopictus* eggs were highly resistant to dry conditions if they were kept in humid conditions for four days before being exposed to drought. The same study recorded a maximum egg longevity of 243 days at 25 °C and a relative humidity of 70%–75%. In another laboratory experiment Hien (1975b) showed that eggs kept on wet cotton wool for four days and then exposed to 25–26 °C air at 60%–70% relative humidity were highly resistant to dryness. After two months under these conditions of exposure, 94.7% of the eggs with conditioned embryos produced larvae. Maximal resistance to desiccation has been observed when eggs were exposed to humidity for at least 24 hours, whereas partial or total mortality has been recorded when eggs less than 16 hours old were dried (references in Hawley, 1988).

A density-dependent factor that appears to play an important role in the survival of *Ae. albopictus* eggs is predation. Gubler (1971a) found that the egg mortality of a natural population of *Ae. albopictus* from Calcutta, India, was greater than 50% during the first 24 hours, primarily as a result of predation by ants. A study conducted in New Orleans, Louisiana, in 1989 examined the survivorship of *Ae. albopictus* eggs in tires (NOMCB, 1989). Eggs for these experiments were obtained from field sources, kept under insectary conditions for five to seven days to favor embryonation and viability, and then returned to the same study areas. Ovistrips were placed in "dry" conditions (tires with holes to prevent flooding) and "wet" conditions (tires filled up with water). The study found that survivorship of the field-collected eggs under both sets of conditions was between 10% and 30% after 24 hours. Thus, the rate of egg loss was between 70% and 90% and quite similar in both "wet" and "dry" conditions. It was presumed that egg loss was caused mainly by predation by other arthropods, such as arachnids, psocids, orthopterans, isopods, and others. The initial loss of eggs occurred when the mean number of intact eggs (to differentiate from collapsed or damaged eggs) per ovistrip was approximately 50 and the eggs were in clumps. The rate of egg loss became negligible when the mean number of intact eggs diminished to about 5 per ovistrip. Thus, the data indicated that egg loss is related to egg density. Egg survival in *Ae. albopictus* appears to depend on small numbers of eggs that avoid predation by being widely spaced.

Like all *Aedes* of the subgenus *Stegomyia*, *Ae. albopictus* females lay their eggs singly and spread them around the container at varying distances from the water surface. Each egg is attached at the water's edge in the meniscus or in the wet zone just above the surface. Amerasinghe and Alagoda (1984) observed that female *Ae. albopictus* follow a set pattern when they oviposit on bamboo traps. About 75% of their eggs are deposited within 16 mm of the water surface, vertically and obliquely, with wide spacing left between singly laid eggs. Oviposition extends to 53 mm above the water level.

Eggs of *Ae. albopictus* hatch when they are exposed to a specific stimulus. After embryonic development has been completed, hatching can occur within minutes of flooding, and larval growth and development can proceed immediately. As a batch of *Ae. albopictus* eggs begins to hatch, the time between the emergence of the first and the last larvae can range from a few minutes to several dozen days depending mainly on water temperature and food availability. A widespread phenomenon within the genus *Aedes*, including *Ae. albopictus*, is that some eggs may hatch readily in response to the stimulus of inundation, while others may remain dormant for varying periods despite being submerged (Edgerly et al., 1993). This phenomenon is known as installment hatching (Gillet, 1971), and is seen in *Ae. albopictus* when a batch of eggs undergoes a mass hatching followed by several additional small hatchings (Gubler, 1971b; Hien, 1975c; Hanson and Craig, 1994).

Another parameter that is important for the hatching of *Ae. albopictus* eggs is the amount of oxygen dissolved in the water. Low oxygen levels, usually associated with high levels of microbial activity and nutrients in the water, increase hatching (Hien, 1975c; Imai and Maeda, 1976; Edgerly et al., 1993). After egg flooding, microorganisms colonize the egg surfaces, resulting in a decrease in dissolved oxygen owing to an increase in metabolic microbial activity; this, in turn, stimulates egg hatching (Edgerly et al., 1993). Thus, larval feeding on microorganisms seems to be a basic mechanism that may inhibit egg hatching. As a result of this observation, studies have focused on larval grazing activity as a possible explanation of interspecific and intraspecific egg hatch inhibition among *Ae. albopictus* and congeneric species (Edgerly et al., 1993). This research is discussed further in the section on competitive interactions.

The effects of egg freezing in *Ae. albopictus*, together with diapause, are discussed in the following section.

Egg Diapause, Photoperiod, and Adaptations

In temperate regions of the world, particularly the *Aedes albopictus*-infested areas of North America and the northernmost points of its distribution in Asia (Japan and China), the species overwinters in the egg state (Ishii et al., 1954; Wang, 1962; Wang, 1966; Imai and Maeda, 1976; Mori and Wada, 1978; Mori et al., 1981). Survival of the northern *Ae. albopictus* depends on all or most of the eggs entering a state of hatching-suppression sufficient to outlast winter. This is a genetically determined property known as diapause. The diapause state is characterized by reduced morphogenesis, increased resistance to environmental extremes, and altered or reduced behavioral activity. All known cases of egg diapause in the Culicidae correspond to suppression of response to hatching stimuli by fully formed first instar larvae within the egg; a state of suspended embryonic development has never been demonstrated.

The phenomenon of diapause is considered to be neurohormonally mediated, resulting in a state of low metabolic activity imposed by a specific stimulus. For *Ae. albopictus* strains from temperate areas, the stimulus appears to be related mainly to photoperiod and temperature, and it is adaptive in nature (Hawley, 1988; Focks et al., 1994). In this case the word "adaptive" means a genetically determined characteristic that enhances the ability of an organism to cope with its environment; adaptation is a process whereby a population is altered in such a way as to be better suited to its environment (Ricklefs, 1979; Futuyma, 1986). Overall, shorter days (<13.5 hours) trigger egg diapause, with low temperatures enhancing the photoperiodic response. Longer days tend to favor continuous nondiapause growth and development.

Other environmental variables such as latitude (geographical origin of the strains) and elevation also play a role in the induction of diapause in *Ae. albopictus*. Geographical variation in the "critical photoperiod" (Cpp—the photoperiod at which 50% of the individuals in the mosquito population produce diapause eggs) has been reported among strains of *Ae. albopictus* from the United States and Japan and is known to vary clinally with latitude (Pumpuni, 1989; Pumpuni et al., 1992). Some modeling studies also indicate that higher elevations are associated with an increased Cpp in *Ae. albopictus* (Focks et al., 1994). Strains of *Ae. albopictus* from the tropics and subtropics do not demonstrate sensitivity to photoperiod. Also, *Ae. albopictus* eggs from tropical areas have not demonstrated overwintering capabilities. For tropical *Ae. albopictus*, survival seems to depend on erratic rather than delayed hatching. *Ae. albopictus* is considered to display facultative diapause.[2] Mori et al. (1981) demonstrated that pupal and adult *Ae. albopictus* are the stages that are sensitive to photoperiod.

The photoperiodic response of *Ae. albopictus* from temperate areas appears to have favored the rapid northerly spread of the species in the central and eastern United States, where it has colonized a vast territory in just a few years. *Ae. albopictus* moved northward from a latitude of 30° N in Houston, Texas, to 42° N in Chicago, Illinois, within three years. This observation also reinforced early conclusions that *Ae. albopictus* from North America have a temperate origin in Asia (Hawley et al., 1987). The northern distribution of *Ae. albopictus* in the United States is clearly limited by cold tolerance. Nawrocki and Hawley (1987) have concluded that the −5 °C January isotherm is

[2]**Diapause** in this case is defined as a period during which growth or development of the insect is spontaneously suspended. In species with **obligatory diapause**, only a single generation per year is found (univoltine species). Some *Aedes* species present this phenomenon at extreme northern and southern latitudes. In species with **facultative diapause**, such as *Ae. albopictus*, multiple generations are possible during the year (multivoltine species). This type of diapause usually occurs at midnorthern and midsouthern latitudes (approximately 35°–65°).

a good predictor of the northernmost distribution of the species in the United States.

By contrast, the southward movement of *Ae. albopictus* has been relatively slow, leading scientists to hypothesize that the temperate origin and associated photoperiodic response of the U.S. populations would prevent their colonization of the Neotropics. For instance, for *Ae. albopictus* populations to remain active in southern Texas and Florida during significant portions of the year, they will require a lowering of the day length threshold or total elimination of the photoperiodic response, because in these regions day lengths for most of the year are less than 13.5 hours. However, rapid selection for both of these features has been noticed in *Ae. albopictus* populations along the southern edge of its Florida distribution, suggesting rapid adaptation to shorter photoperiods (O'Meara et al., 1993). A theoretical explanation for this phenomenon could resemble the following scenario: A temperate-zone population transported to a warmer location (southern areas of Texas or Florida) would experience a combination of short day lengths and favorable temperatures for egg and larval development for part of the year. During these periods, nonphotoperiodic *Ae. albopictus* genotypes would multiply, while photoperiodic genotypes would remain as diapausing eggs. Thus, the transformation of a photoperiodic population into a nonphotoperiodic one requires no mutation, but merely a change in gene frequency.

In the laboratory, selection of nonphotoperiodic *Ae. albopictus* from an originally photoperiodic population has been accomplished within seven generations. In natural populations of *Ae. albopictus* from southern Texas and Florida, the ability to diapause has been lost over a three-year period (Craig, 1993). This indicates that the selection for loss of photosensitivity is a phenomenon of southern latitudes. *Ae. albopictus*' invasion of the southern United States (i.e., peninsular Florida) began slowly in comparison to its northern and eastern expansion. The genes had to change via natural selection. Now the species has lost its ability to diapause, and the southern populations of Texas and Florida are analogous to their tropical ancestors and different from their temperate antecedents of the 1980s. It is clear that the species is already in a position to invade any area of Neotropical America, and the process may already have begun (i.e., northern Mexico and the Dominican Republic).

Finally, also in regard to the photoperiodic response, a strain from Cariacica City, Brazil, showed no sensitivity to any photoperiod. Based on this observation, Hawley and co-workers (1987) hypothesized that all strains from the United States might have a common origin in northern Asia (probably Japan), while those introduced into Brazil had a different origin (likely a tropical one). However, recent studies based on allozyme analysis indicated that the U.S. and Brazilian populations appear to share a common origin, with the evidence pointing to northern Japan (Kambhampati et al., 1991). A more recent publication by Hawley reinforced the assumption that the Brazilian populations may share a temperate common ancestor with the U.S. populations (Hawley, 1991).

Egg Cold Hardiness

The ability of an insect to survive suboptimal temperatures is known as "cold hardiness" (Hanson, 1991). Cold hardiness plays an important role in the life cycle of several insects inasmuch as it affects factors such as adaptation to seasonal changes, long-term population fluctuations, and the geographical distribution and colonization trends of invading species.

It is well accepted that there are two different types of cold-hardy insects: freeze avoiding and freeze tolerant. Freeze-avoiding insects produce antifreezes such as low-molecular-weight carbohydrates, polyols, and thermal hysteresis proteins, and may also discard ice-nucleating substances to decrease their supercooling points (SCP). The SCP of an insect is the temperature at which it freezes. Freeze-tolerant insects survive by producing ice-nucleating agents that increase their SCP by inducing ice formation. Low-molecular-weight sugars and polyols are common to both freeze-avoiding and freeze-tolerant insects. Glycerol seems to be the most frequently encountered substance of this type (Somme, 1982). It appears that the most common stimulus for cold hardiness is low temperature (0–5 °C) (Baust and Lee, 1981; Horwath and Duman, 1983; Kukal et al., 1989). Other environmental factors associated with this phenomenon are photoperiodic diapause (Lee and Denlinger, 1985), desiccation (Patterson and Duman, 1978), diet (Knight and Bale, 1986), thermoperiod (Horwath and Duman, 1986), and anoxia or hypoxia (Somme, 1966).

Cold-hardiness studies have focused on eggs of several orders of the class Insecta, particularly those of the order Diptera. All insect eggs studied to date are freeze avoiding. Egg cold hardiness studies have been carried out in several species of the genus *Aedes*, including *Ae. albopictus* (Hatchett, 1946; Hawley et al., 1987; Copeland and Craig, 1990; Hanson, 1991).

Hawley et al. (1987) found that eggs of *Ae. albopictus* from northern Asia and the United States were more cold tolerant than eggs from tropical sites. In this study eggs were subjected to −10 °C for 24 hours, a treatment that killed all *Aedes aegypti* and tropical *Ae. albopictus*; U.S. strains, however, showed a hatch rate of 80%–90%. Eggs placed outdoors in South Bend, Indiana, in mid-October 1986 showed a survival rate of 100% in mid-February 1987. These studies clearly demonstrated that the species overwinters in the northern United States and that cold acclimation and diapause increase the cold hardiness of temperate *Ae. albopictus* strains (Hawley et al., 1989).

Laboratory studies based on genetic crosses between temperate and tropical strains of *Ae. albopictus* showed that hybrid eggs with a temperate female parent are 36% more cold hardy than those with a tropical female parent (Hanson, 1991). The male parent does influence the trait but appears to play a lesser role. The results suggest that the mode of inheritance of cold hardiness "is under maternal influence by either cytoplasmic or sex-linked factors" (Hanson, 1991).

A set of experiments carried out in East St. Louis, Illinois, which were designed to insert genes to reduce the overwintering ability of *Ae. albopictus* field strains, produced a decrease in cold hardiness and diapause incidence in the populations (Hanson, 1991). In the studies, males from a tropical strain of *Ae. albopictus* with a distinctive isozyme marker were released. Subsequent egg samples from the release site showed high (24%) frequency of the genetic marker accompanied by reduced cold hardiness of the field populations. These experiments may open the way for genetic control of *Ae. albopictus* in the colder parts of its range.

All in all, cold acclimation and diapause enhance the cold hardiness of only temperate strains of *Ae. albopictus*.

Egg Morphology

The eggs of *Ae. albopictus* are cigar-shaped, like those of *Ae. aegypti*, and devoid of floats. Egg morphology, based on scanning electron microscopy observations, is as follows: Eggs measure an average of 609.8 μm (± 5.9) in length and 192.9 μm (± 2.4) in width (Linley, 1989). They have "large, central outer chorionic tubercles smoothly rounded, with surrounding cell fields almost invariably devoid of small tubercles, leaving a distinct clear area around each large tubercle," as shown in Figure 1 (Linley, 1989). For purposes of comparing the structure of the eggs of the two species of subgenus *Stegomyia* in the Americas, an electron micrograph of an *Ae. aegypti* egg shows the outer chorionic tubercles surrounded by a fairly narrow, featureless ring (Figure 2). *Ae. albopictus* eggs are blunt at the anterior end and more tapering in the posterior region. The ventral margin is more crescentic than the dorsal margin and has a conspicuous micropylar collar that is moderately prominent, as compared with the very prominent one found in *Ae. aegypti* (Linley, 1989). This characteristic visibly differentiates the two species.

Larvae

Under natural conditions *Ae. albopictus* larvae can develop in water with low turbidity and at a pH ranging from 5.2 to 7.6, with optimal pH between 6.8 and 7.6 in Asia (Ho et al., 1972). Water containing amino acids, ammonia, and, in general, a high organic nitrogen content appears to

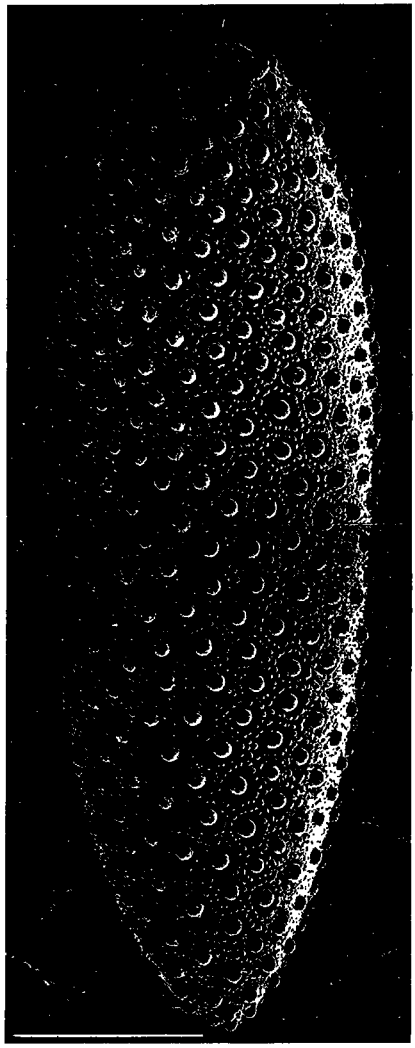


Figure 1. Electron micrograph of entire egg of *Aedes albopictus*. Scale: bar = 100 μm. (Photo by Dr. John Linley, Florida Medical Entomology Laboratory, University of Florida at Vero Beach.)

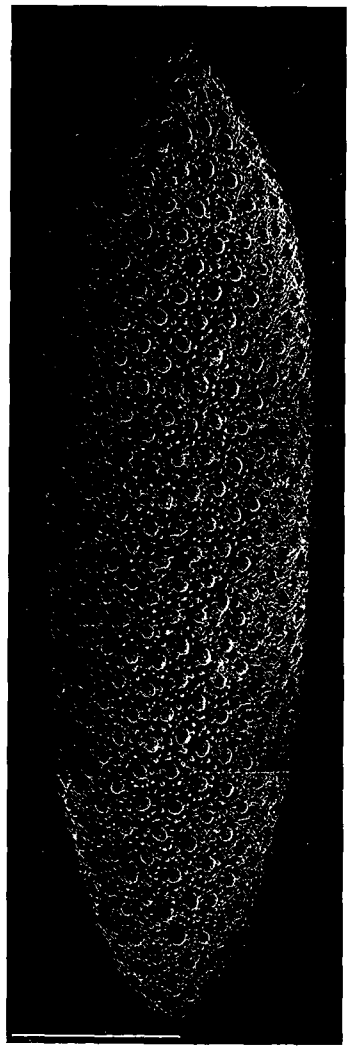


Figure 2. Electron micrograph of entire egg of *Aedes aegypti*. Scale: bar = 100 μm. (Photo by Dr. John Linley, Florida Medical Entomology Laboratory, University of Florida at Vero Beach.)

be the ideal habitat for *Ae. albopictus* (Laird, 1959). To assess the effects of pH on fourth instar *Ae. albopictus* larvae, laboratory studies were conducted with colonized strains in New Orleans. Larvae were tested to determine their tolerance to various pH levels. The results showed that a pH equal to or more acid than 2.0, or equal to or more alkaline than 12.0, is fatal to mature larvae after a four-hour exposure (NOMCB, 1987). The studies also reconfirmed the observation that the species is able to survive in water containing relatively high concentrations of strong electrolytes. Measurements in the natural larval habitats of the strains in the New Orleans study showed pH ranges of 6.33–8.35 for tires and 6.43–8.23 for tree holes.

Larvae have been known to survive ranges of dissolved oxygen of 3–6 ppm in a variety of habitats (Ho et al., 1972). Much lower survival ranges have been observed in the tree holes of New Orleans (sugarberry and red maples), which had a narrower range of 0.6–2.7 ppm. Also, the larvae have been found alive at values as low as 1.3 ppm of dissolved oxygen in tire yards in New Orleans (NOMCB, 1987).

Adaptability to varied habitats enables the species to breed successfully in a wide variety of water-retaining containers. It also appears that *Ae. albopictus* larvae are even more tolerant of water with a high organic content than are *Ae. aegypti* larvae, although the latter species has now been reported from highly organic water conditions such as are found in tree holes, septic tanks, soak away pits, and the like.

Larval size and the duration of larval development are influenced by temperature, food supply, crowding, and sex. Under laboratory conditions, Hien (1975a) demonstrated that temperature affects the duration of larval development. At 30 °C development took 6 days, while at 25 °C and 20 °C, it took 9 and 13 days, respectively. Laboratory studies of the Brazilian strains have shown a larval developmental period ranging from 4 to 9 days at a temperature of 25 °C (Xavier et al., 1991). Hien (1975a) also demonstrated that the fourth larval instar period is the longest and that the effect of temperature is clearly defined for that stage.

Regarding the effect of food supply, starvation extends the larval development period to an average of 42 days, with an 80% mortality rate. One of the findings of Hien (1975a) was that *Ae. albopictus* can successfully fast for long periods of time. Thirty-five percent of 100 specimens emerged from larvae that had been starved during the first three developmental stages.

Under natural and artificial conditions, high larval density appears to produce high mortality and an increase in larval development time. In comparison to *Ae. aegypti*, however, *Ae. albopictus* was more resistant to crowding (Hien, 1975a; Mori and Wada, 1978).

Livingstone and Krishnamoorthy (1982), conducting laboratory experiments with *Ae. albopictus* larvae in India, demonstrated that the larval period of females (119–149 hours) was greater than that of males (115–141 hours).

Larval Seasonal Prevalence

Larval seasonal prevalence of *Ae. albopictus* appeared to be closely related to rainfall. Studies in Singapore (Ho et al., 1971), Bangladesh (Azzizar, 1980), Japan (Toma et al., 1982; Sota et al., 1992), and the United States (NOMCB, 1987; NOMCB, 1988) have shown that the species is abundant during the rainy season. It is important to point out that since *Ae. albopictus'* range extends from the tropics to the temperate zone, seasonal peaks will differ with area.

In a representative area of the tropics such as the city of Singapore, *Ae. albopictus* presents three well-defined larval population peaks: December, April–May, and August–September. The population peaks of the larvae precede those of the adults by almost exactly two months (Ho et al., 1971). In temperate regions, such as northern Japan, larvae of *Ae. albopictus* are present from late March through mid-September. High larval population peaks have been observed in July–August and October, shortly after the rainfall peaks (Toma et al., 1982; Sota et al., 1992). High larval mortality has been observed to occur in the winter (Makiya, 1973; Mori and Wada, 1978; Mori et al., 1981).

In Okinawajima Island in the Japanese subtropics, a large peak in the larval population was observed from June to mid-July, and the population became very low during November through March. Larvae were collected every month of the year (Toma et al., 1982).

Studies in the United States conducted in New Orleans in tire yards and tree hole habitats during the summer of 1987 indicated that the abundance of *Ae. albopictus* larvae peaked in June (almost simultaneously with rainfall peaks) and decreased gradually through August (NOMCB, 1987). Conversely, maximum larval production in tree holes in areas of the Paraiba Valley, São Paulo, Brazil, does not appear to coincide with rainfall peaks (Gomes et al., 1992). The highest larval production was observed in the months of March and April, which correspond to the fall season in the Southern Hemisphere.

Larval Morphology

Microscopic examination is necessary to identify *Ae. albopictus* larvae and differentiate them from other *Aedes* species, especially *Aedes aegypti* larvae. The most significant differences between *Ae. aegypti* and *Ae. albopictus*, which sometimes share the same habitat, are the following: On the mesothorax and metathorax, *Ae. albopictus* has pleural hair groups that lack the long spines found in *Ae. aegypti*. In *Ae. albopictus* there are two branches in seta 7-C on the head, while *Ae. aegypti* has only one. The ventral brush of *Ae. albopictus* has four pairs of hairs, whereas *Ae. aegypti's* brush has five pairs. *Ae. albopictus* comb scales have a bare apical spine and a row of small spinules basally on each side, while *Ae. aegypti's* comb scales present several shorter, stout, subapical spines (Huang, 1972) (see Figure 3).

Larval Habitat

Ae. albopictus is a container breeder. It breeds in both natural and artificial receptacles. *Ae. albopictus* has been found breeding in such natural habitats as tree holes, bamboo holes and stumps, coconut shells, plant axils (bromeliads), ground pools, and rock pools. Its artificial habitats include rubber tires, tin cans, drums, earthenware containers, bottles, flower pots, cisterns, and buckets.

In the continental United States, infestations of *Ae. albopictus* have been found in used tire stockpiles, salvage yards, illegal dumps, the premises of tire dealers working with trucks and large equipment, and tire retreaders. Surveillance conducted in residential areas of the United States has also reported infestations in tin cans, bird baths, clogged rain gutters, water bowls for pets, buckets, plastic and metal containers holding rainwater, and cemetery flower pots (Moore et al., 1988; O'Meara and Gettman, 1991). Natural containers such as tree holes and tank bromeliads appear to be among the preferred habitats of *Ae. albopictus* larvae in suburban settings of the United States and Brazil (NOMCB, 1987; O'Meara et al., 1993; Gomes et al., 1992). Recent reports from the Dominican Republic have determined that tree holes, rock holes, and fast-food containers are the main larval breeding places. Tree holes of *Celtis laevigata*, a species of sugarberry, are one of the main breeding habitats of the species in New Orleans, Louisiana (NOMCB, 1987). Examples of larval breeding places for *Ae. albopictus* from the United States are presented in Figures 4 to 14.

Preferred natural larval habitats in various countries of Asia are bamboo stumps, coconut shells, rock holes, and ground pools (La Casse and Yamaguti, 1950; Hong et al., 1971; Harrison et al., 1972; Ho et al., 1972; Huang, 1972; Rozeboom and Bridges, 1972; Miyagi et al., 1983). In countries of Southeast Asia other major breeding habitats include earthenware, tin cans, ant traps,[3] rubber tires, bowls, and drums. Ant traps are the most common indoor habitat in places such as Singapore, Dacca, and urban areas of Malaysia (Ho et al., 1972; Azzizar, 1980; Chan, 1985).

Landscape tank bromeliads have been studied as breeding places for *Ae. albopictus* in a number of locations in central and southern Florida in the United States (O'Meara et al., 1993). In the northern latitudes of Florida, immature *Ae. albopictus* have been recovered from *Aechmea distichantha*, a cold-hardy tank bromeliad, which grows in central Florida in the city of Gainesville (29°40′ N latitude). Before *Ae. albopictus* became established in the area, the

[3]Small ceramic jars filled with water placed under the legs of meat safes in houses without refrigerators.

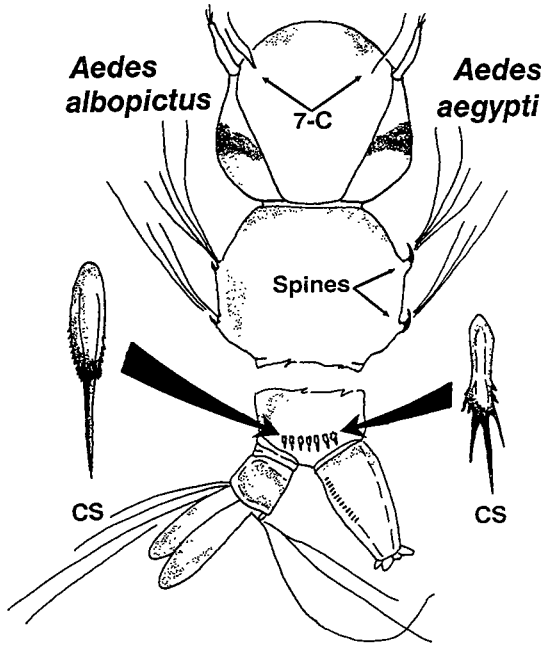


Figure 3. Drawing illustrating the most important differences between *Aedes albopictus* and *Aedes aegypti* larval stages. (Drawing provided by Dr. George O'Meara, Medical Entomology Laboratory, University of Florida at Vero Beach.)

bromeliad was the dominant microhabitat for *Wyeomyia* spp. It now appears that *Ae. albopictus* is the main species in *Aechmea distichantha*, replacing other culicids. The species has been found in more than 70% of all bromeliads sampled in the Gainesville studies. This observation appears to have been influenced by the fact that many other species of tank bromeliads were killed or severely damaged by a hard freeze. Two months after the freeze and for a period of more than 15 months, *Ae. albopictus* was the only species recovered from the cold-hardy tank bromeliad. Thus, because of the cold winter, and in the absence of *Wyeomyia*, *Ae. albopictus* is the dominant species (O'Meara et al., 1993).

Farther south of Gainesville in Vero Beach, Florida (27°40′ latitude), *Ae. albopictus* larvae have been found in other bromeliads such as *Neoregalia spectabilis*, *Billbergia pyramidalis*, and *Aechmea fasciatus*. In these microhabitats *Ae. albopictus* was collected from fewer than 10% of the plants sampled, while *Wyeomyia* spp. were found in nearly 90% of the bromeliads sampled. Thus, the main culicids at this site are *Wyeomyia* spp. (O'Meara et al., 1993).

In countries of tropical Asia, the breeding preferences of *Ae. albopictus* in plant axils include leaves of *Pandanus* and banana trees and leaves of *Colocasis esculenta* (taro) (Kurihara, 1984).

A study conducted by Laird (1959) in several areas of the city of Singapore described some of the characteristics of the larval microhabitat of *Ae. albopictus* where the larvae had optimum development. In relation to the aquatic flora and fauna, the water of the larval habitat was classified as α or β mesosaprobic. β mesosaprobic waters supported a rich and diverse flora and fauna consisting of several spe-

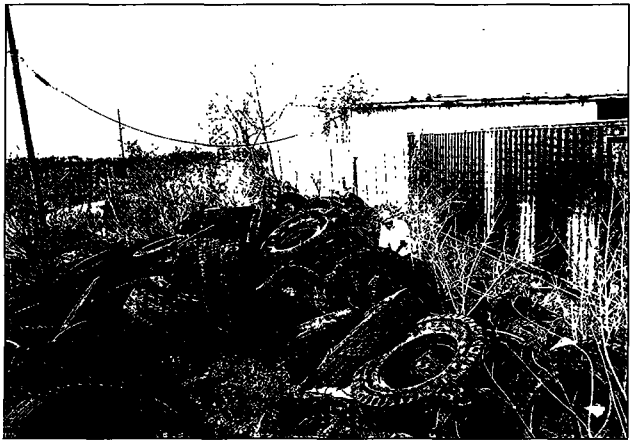


Figure 4. *Aedes albopictus*-infested tires, Houston, Texas, U.S.A., March 1986. (Photo by Dr. C. G. Moore, Division of Vector-Borne Infectious Diseases [DVBID], CDC.)

Figure 5. Placement of a CDC ovitrap for *Ae. albopictus* surveillance (Photo by Dr. C. G. Moore, DVBID, CDC.)

Figure 6. Tree hole containing water and *Ae. albopictus* larvae, New Orleans, Louisiana, U.S.A. (Photo by Dr. J. E. Freier, DVBID, CDC.)

Figure 7. Bottle with water and *Ae. albopictus* larvae. (Photo by Dr. C. G. Moore, DVBID, CDC.)

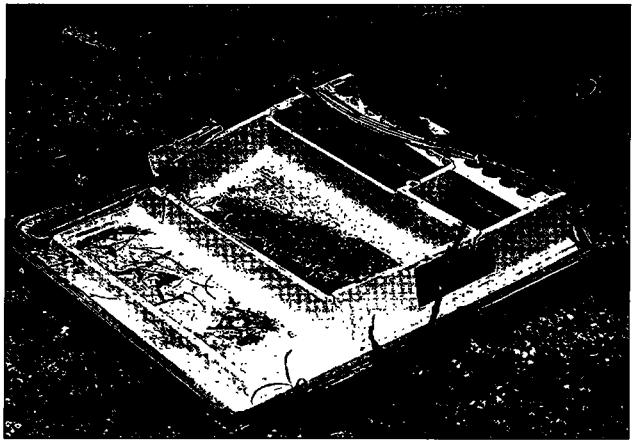


Figure 8. Discarded refrigerator door, with water and leaf litter infested with *Ae. albopictus* larvae, New Orleans, Louisiana, U.S.A. (Photo by Dr. J. E. Freier, DVBID, CDC.)

Figure 9. Checking for adult *Ae. albopictus* at a used tire retread facility, Atlanta, Georgia, U.S.A. (Photo by Dr. C. G. Moore, DVBID, CDC).

Figure 10. *Aedes albopictus* **larvae in a discarded toilet bowl filled with water. (Photo by Dr. C. G. Moore, DVBID, CDC.)**

Figure 11. *Aedes albopictus* **larvae in plastic sheet with water and leaf litter. Note adjacent tire casing also containing water. New Orleans, Louisiana, U.S.A. (Photo by Dr. J. G. Freier, DVBID, CDC.)**

Figure 12. Miscellaneous container habitats for mosquitoes, infested with *Ae. albopictus* larvae. (Photo by Dr. C. G. Moore, DVBID, CDC.)

cies of diatoms, desmids, microcrustaceans, phytoflagellates (Euglenaceae), ciliates, and many different rotifers, cyclopoids, ostracods, and decapods. All of the above provided ideal conditions for development of *Ae. albopictus* because of the abundance of food and the relatively low concentration of deleterious substances. The α mesosaprobic habitat was less well suited for *Ae. albopictus* development; nevertheless, substantial densities of *Ae. albopictus* larvae were found. That water contained free-living green algae, blue-green algae (*Oscillatoria*), flagellates, phytoflagellates (*Euglena*), *Paramecium*, vorticellas, and some rotifers. The crustacean fauna was abundant in cyclopoids and cladocerans.

Larval Pathogens and Predators

Several pathogens and predators of *Ae. albopictus* larvae have been described in the literature.

The fungus *Coelomomyces stegomyiae* was found on several *Ae. albopictus* larvae in Singapore. The second instar larvae showed the heaviest infections, concentrated in the head capsule, thorax, and anal papillae (Laird, 1959). High infection rates in experimental trials with *Coelomomyces stegomyiae* var. *chapmani* have demonstrated the potential of the fungus to serve as a biological control agent for *Ae. albopictus* as well as other Culicidae (Lien and Lin, 1990). The infection process of *Ae. albopictus* larvae by another fungus, *Tolypocladium cylyndrosporum*, has also been described. The pathogenesis of the fungal invasion of the exoskeleton and the digestive apparatus of the larvae has been studied to some extent, but the potential use of this fungus as a biological control agent for the species is not yet clear (Ravallec et al., 1989).

A gregarine protozoan parasite, *Lankesteria culicis* (= *Ascogregarina taiwanensis* Lien & Levine, 1980) is known to develop trophozoites in the cells lining the larval midgut of *Aedes albopictus* (Huang, 1972). Recent studies conducted in Illinois (Munstermann and Wesson, 1990) have demonstrated the presence of *Asc. taiwanensis* in strains of *Ae. albopictus* from North America. Field-collected specimens showed infection rates of 67% to 95% at four sampling sites; subsequent isolations of the parasite from field-collected *Ae. albopictus* hosts seem to show some pathogenicity in the larvae and pupae of laboratory strains of *Ae. albopictus*. In general, although the gregarine protozoan has little effect on its natural host, it does appear to have a marked deleterious effect on indigenous mosquitoes of North America such as *Ae. aegypti* and *Ae. atropalpus* (see the discussion on parasitism in the section on competition studies). Also, the study reports some strain variation in susceptibility to infection among the different North American *Ae. albopictus* populations. This study is the first to find this gregarine protozoan in culicid larvae in North America.

Some workers have reported experimental infections of *Ae. albopictus* larvae with the nematode *Romanomermis culicivorax* (Petersen and Chapman, 1979; Blackmore, 1992). So far, parasitism of *Ae. albopictus* by mermithid nematodes has not been reported in any natural populations of the species. The laboratory studies mentioned above have shown intermediate infection rates in North American strains of *Ae. albopictus*. Mermithids are known to infect larval mosquitoes by penetrating the cuticle and subsequently maturing in the hemocoel of the host.

Laird (1959) also found a variety of other pathogens, such as the ciliates *Tetrahymena pyriformis* and *Epistylis lacustris*, the alga *Oscillatoria brevis*, and the bacterium *Sphaerotilus dichotomus*.

In regard to predators, Marten (1984) observed a copepod predator, *Mesocyclops leuckarti pilosa*, feeding upon first instar larvae of *Ae. albopictus*. The copepod was capable of eliminating them entirely. A drawback to the use of this predator is that it appears to be scarce in *Ae. albopictus* habitats. Further research conducted by the same in-

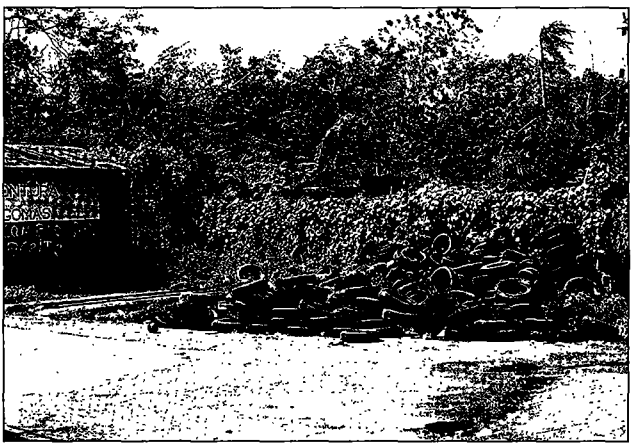


Figure 13. Discarded tires as a potential *Ae. albopictus* breeding site. (Photo by Dr. C. G. Moore, DVBID, CDC.)

Figure 14. Inspection of tire casings from Asia for *Ae. albopictus* larvae. (Photo by R. E. Schoeppner, San Mateo Mosquito Abatement District, Burlingame, California, U.S.A.)

vestigator has demonstrated the successful use of other species of larvivorous copepods in controlling *Ae. albopictus* larvae in tire piles. In a period of 8–10 weeks the crustacean *Macrocyclops albidus* (Jurine), a species with broad distribution in the Americas, was able to completely eliminate larvae in tire piles found in and around New Orleans (Marten, 1989a; 1989b; 1990a; 1990b). Marten also discusses the use of mixtures of several species of cyclopoid copepods to control species of *Stegomyia* and other culicids of medical importance and these copepods' potential effect on larval aquatic habitats. The mixtures of *Macrocyclops albidus* and *Mesocyclops ruttneri,* both collected in natural habitats in New Orleans, proved to be as effective as *Macrocyclops* by itself. An advantage of this approach was the increase in survival rates of both species in the mixture, compared to the survival rate when a single species was introduced (Marten, 1990b).

Finally, various *Toxorynchites* mosquito species are known to prey on *Ae. albopictus* larvae. One of these predators that has been found breeding successfully with *Ae. albopictus* larvae in Asia is *Toxorynchites splendens* (Surtees, 1966). It appears that some *Toxorynchites* spp. may be effective in controlling *Ae. albopictus* larvae. Two species of *Toxorynchites*, one introduced (*amboinensis*) and the other indigenous (*rutilus septentrionalis*), have been massively produced in insectaries, and control trials are being carried out in areas of New Orleans to test their efficacy in the field (Freier, pers. comm., 1993).

Pupae

Under ideal conditions, *Ae. albopictus* remains in the pupal stage for about two days (Sheng and Wu, 1951; Surtees, 1966; Hien, 1975a), and, as in other *Aedes* species, *Ae. albopictus* males emerge before females. Livingstone and Krishnamoorthy (1982) showed that the pupal development period was 32–36 hours for males, while females reached the adult stage in 49–52 hours. The same experiment suggested that pupal development of females requires a minimum dark period of 12 hours.

Hien (1975a) studied the effect of water temperature on pupal development. The results showed that pupal development lasted two days at 30 °C, three days at 25 °C, and five days at 20 °C. *Ae. albopictus* pupae survive desiccation for up to two days at 26 °C and a relative humidity of 87%. Pupal mortality was about 1% under field conditions (Ho et al., 1972).

Adults

Longevity

Studies of longevity (survival) in different populations of vector mosquitoes (particularly females) often provide important epidemiologic information, because greater longevity increases the probability of transmitting diseases. One of the most important questions concerning *Ae. albopictus* is whether adult females of this species are capable of living long enough to become infected and subsequently transmit infectious agents. Studies of male survival may also be important, especially in the application of certain genetic control measures. In addition, survival data may be useful in the assessment and administration of vector control operations.

The bulk of the data on longevity of *Ae. albopictus* adults (survival studies) comes from laboratory research (reported in Hawley, 1988). Few studies have attempted to estimate longevity of *Ae. albopictus* adults in the field. Thus far, two studies have been carried out with North American strains. Some of these laboratory and field studies are described below.

Environmental factors stimulate responses that greatly modify the behavior and biology of the adult mosquito. Temperature and relative humidity are among the factors that play a vital role in adult survival. Gao et al. (1984) reported that during eight years of observations of caged *Ae. albopictus* (kept at temperature conditions of 25 ± 1 °C and a relative humidity of 80 ± 5%), the maximum longevity of the adult females was 30–40 days. The same study demonstrated that the upper thermal survival limit was 40 °C (LT_{50} = 0.9 hour) and the lower limit was −5 °C (LT_{50} = 0.85 hour).

Hylton (1969) showed that longevity of the adult *Ae. albopictus* female reached about 84 days at a temperature of 22.2 °C and relative humidity of 80%. *Ae. albopictus* was tolerant of low temperatures (15.5 °C) and high and low humidities, whereas high temperatures (32.2 °C) decreased survival, independent of the relative humidity. It appears that the ability of *Ae. albopictus* to survive various temperatures and humidities may have favored its distribution in climatic conditions that range from temperate to tropical. It has been suggested that *Ae. albopictus* conserves body fluids at low humidities, thereby preventing tissue desiccation, through spiracular control or another moisture regulating mechanism (Hylton, 1967).

Longevity in the laboratory is also affected by feeding. Gubler and Bhattacharya (1971) maintained mosquitoes at a temperature of 26 °C and a relative humidity of 50%–60%, and demonstrated that blood-nourished *Ae. albopictus* females lived from 38 to 112 days. A maximum of 117 days was found by Hien (1976a).

By contrast, mosquitoes that were fed with water and kept at temperatures of 25–26 °C and 60%–70% relative humidity began to die after three days. The majority of starving *Ae. albopictus* did not live longer than five to seven days (Hien, 1976a). Under natural conditions a female would normally find a suitable host before this time interval elapsed.

There are two general approaches for measuring the rate of survival in insects: indirect methods based on physio-

logical age within a population and direct estimates by mark-release-recapture experiments (Service, 1976).

Indirect methods to assess female survival are based chiefly on tracheation of the ovaries and ovariolar dilatations (Polovodova, 1949; Detinova, 1962). Analysis of the tracheation of the ovarioles yields the parity rate, i.e., the proportion of the population that has oviposited. Therefore, the mosquito population can be separated into two groups: an older group with one or more oviposition cycle (parous) and a younger group with no oviposition cycle (nulliparous). The greater the proportion of parous females, the older the population. Parity rates are determined by dissecting the ovaries of unfed or recently fed females and examining them for the presence or absence of clumped or coiled tracheoles. If the tracheoles are coiled, the female is nulliparous; if they are not coiled, the female is parous. Parity rates are important for comparing the age of populations of different species in different seasons or after insecticide treatment. Most important, if the oviposition cycle or the gonadotrophic cycle is known, both the daily survival rate (proportion surviving through one day) and the average age of the population can be estimated mathematically. The daily survival rate p is estimated by extracting from the proportion of parous females the root equal to the number of days in the oviposition cycle. The formula is as follows: $p = \sqrt[x]{\text{proportion of parous females}}$, where x = the oviposition cycle in days. The ovariolar dilatation method determines the number of times that a female mosquito has oviposited by examining dilatations in the basal part of the follicular tube (pedicel), a small duct that connects each ovariole in the ovary to the lateral oviduct (calix). Each oviposition produces a dilatation; thus, the number of dilatations found in the follicular tubes of an ovary indicates the number of times the mosquito has oviposited. The number of ovipositions indicates the physiological age of the mosquito, which, when multiplied by the estimated number of days in the oviposition cycle, yields an estimate of the chronological age.

Estimates of adult longevity of *Ae. albopictus* based on ovariolar dilatations and tracheation of the ovaries have been carried out in several laboratory studies. Hawley (1988) discusses their shortcomings, pointing out that age may be underestimated when the estimate is based on ovariolar dilatations. For instance, some studies have shown that *Ae. albopictus* females do indeed form recognizable dilatations, but that their number does not equal the known number of gonotrophic cycles completed. Most of the estimates of daily survival based on the assessment of parity rates of *Ae. albopictus* have been conducted with Asian strains. The results displayed p values ranging from 0.71 to 0.88, which correspond to an average female longevity of 2.9 to 7.8 days (Hawley, 1988). The average longevity of the population is calculated by taking the reciprocal of the negative natural logarithm of p, so that life expectancy = $1/-\ln p$.

Mark-release-recapture methods used to directly estimate survival usually involve marking a known number of individuals with various dyes, releasing them into the wild, and then trying to recapture them by different means. A regression line is then constructed by plotting the values of the $\log_{10}$(recaptures + 1) against the number of days post-release. Next, the slope of the regression is calculated in a simple way to obtain the probability of daily survival, p (Walker et al., 1987). The antilog of the regression coefficient yields the daily survival rate. Aside from being of chief importance in survival studies, direct methods, such as mark-recapture analysis, are also used for the following purposes: to estimate adult densities; to measure dispersal; to determine the timing of reproductive events; to evaluate the extent to which an individual vector returns to the same species for its blood source; and to identify resting places, especially outdoors and during the season of minimum density.

In Singapore the oldest females collected in houses and on human baits had undergone three gonotrophic cycles, suggesting a period no greater than 11 days, while in Calcutta dissections of wild females showed only one or two ovipositions, indicating an even shorter life-span than in Singapore (Ho et al., 1972; Gubler and Bhattacharya, 1971). Some other studies have reported collection of marked *Ae. albopictus* females at periods greater than 20 days postrelease (Bonnet and Worchester, 1946; Rosen et al., 1976; Niebylski, 1992).

Mark-release-recapture studies conducted with North American *Ae. albopictus* strains in the eastern part of the city of New Orleans during the rainy season of 1987 showed an overall average probability of daily survival of 0.77 for both males and females (NOMCB, 1987). Thus, the life expectancy value for the population was about four days. More recent research, also from North America, was carried out in a tire yard in Potosi, Missouri, during 1989–1991 and showed higher survival rates for *Ae. albopictus* females than those reported in other studies. In this research the p value for females was 0.89, which corresponds to 8.6 (or about 9) days life expectancy in this population (Niebylski, 1992). In this particular study, a single female was observed to survive 24 days. The survival rate p of the adult males was 0.77, which is comparable to the values reported by other researchers. An average 8-day survival of *Ae. albopictus* females combined with an average gonotrophic cycle of four days means that *Ae. albopictus* potentially will take two blood meals in a lifetime, increasing the vectorial potential of the species.

Mating Characteristics

As stated before, cross-specific mating between *Ae. albopictus* and other species has been observed. The phenom-

enon, a form of competition for mates, is known as satyrism, and it has been noticed in laboratory experiments and in the field, particularly with male *Ae. albopictus*. Furthermore, it is known that injections of matrone, the *Ae. albopictus* male accessory gland pheromone, renders the female *Ae. aegypti* refractory to subsequent inseminations (Ali and Rozeboom, 1973; Nasci et al., 1989; Craig, 1993). On the other hand, matrone from male *Ae. aegypti* has no effect on female *Ae. albopictus*. It is believed that the proficiency of the *Ae. albopictus* males in mating with other species could be involved in the dramatic displacement trends of *Ae. aegypti* by the *Ae. albopictus* populations in the southern United States (Nasci et al., 1989).

Natural mating behavior of *Ae. albopictus* was reported in a Calcutta study (Gubler and Bhattacharya, 1972). It was found that male *Ae. albopictus* swarmed around the feet and ankles of a human observer. Female *Ae. albopictus* arrived later and were mated as they approached the host to feed. Mating took place in flight and usually occurred within one to three feet of the ground. Most of the matings lasted from 5 to 15 seconds. A majority of the copulating females that were captured were nulliparous, and most were inseminated in the vicinity of the host. The same study also reported swarming of males at the bases of trees and over metal baskets, leading to some copulation and insemination of females. It has been reported that one copulation is sufficient to fertilize one batch of eggs and that females are not inseminated until they are 30 to 36 hours old (Ho et al., 1972).

Oviposition

The speed of egg production, like that of other physiological processes of insects, is critically dependent on environmental factors such as temperature.

The underlying mechanism that triggers oviposition in *Ae. albopictus* has been studied to some extent in strains from India and from Lake Charles, Louisiana, in the United States (Leahy and Craig. 1965; Klowden and Chambers, 1992; Klowden, 1993). Experimental studies have indicated that male accessory gland components of *Ae. albopictus* play a role in inducing egg deposition in the females (Leahy and Craig, 1965; Klowden, 1993). It appears that the oviposition stimulant for females is not related to the mechanics of mating but rather to stimulant substances produced by the male accessory gland. Likewise, abdominal distention resulting from a blood meal seems to provide a second stimulus that initiates ovarian development (Klowden, 1993).

Although it is generally accepted that *Ae. albopictus* females begin to feed two days after emergence (Del Rosario, 1963; Gubler and Bhattacharya, 1971; Hawley, 1988), some *Ae. albopictus* have been observed to take their first blood meal during their first day postemergence (Hien, 1976b). Hien (1976b) observed that *Ae. albopictus* females were ready to take blood meals several times during a single gonotrophic cycle, that is, on the second and third days after the first meal. Gubler and Bhattacharya (1971) also observed that *Ae. albopictus* females took blood for a second time in a single gonotrophic cycle. Multiple feeding during one gonotrophic cycle could be an important component in the epidemiology of vector-borne diseases (Burkot et al., 1988). This behavior could increase the ability of *Ae. albopictus* to acquire and deliver infections from and to different hosts, thereby spreading pathogens to a larger susceptible human population. Information regarding *Ae. albopictus* feeding patterns is sketchy; however, it is known that the species has a wide host range compared with other *Stegomyia* species. Thus, there is a real possibility that *Ae. albopictus* may pick up pathogens in a zoonotic cycle and carry them to humans in the domestic environment.

Knowledge of the interval between successive ovipositions (the duration of the gonotrophic cycle) allows conversion of the physiological age into a longevity measure for the population and also the study of population dynamics. In general, *Ae. albopictus* laboratory experiments seem to agree with field studies, pointing to an average duration of five days for the first and second gonotrophic cycles. For instance, Mori and Wada (1977) demonstrated that under natural conditions, with an average field temperature of 25 °C, the period from emergence to the first blood meal of *Ae. albopictus* was about two days and the duration of one gonotrophic cycle was five days. These results were in accord with laboratory experiments. Using Detinova's method, the same studies showed that *Ae. albopictus* females are ready to feed again within 24 hours after oviposition.

Under laboratory conditions, Del Rosario (1963) found that the first blood meal was taken two days after emergence, and the gonotrophic cycle was found to last three to four days before oviposition at a temperature of 24–29 °C and 80%–93% relative humidity. Gubler and Bhattacharya (1971) also observed that the first blood meal of *Ae. albopictus* females took place two days after emergence, with a gonotrophic cycle lasting three to five days after a blood meal at a temperature of 25–26 °C and relative humidity of 50%–60%. Hien (1976b) showed that the gonotrophic cycle after a blood meal lasted three to three-and-a-half days at a temperature of 25–26 °C and a relative humidity of 60%–70%.

The number of eggs laid by *Ae. albopictus* depends on the physiological age of the mosquito, the body weight after emergence, and, particularly, the size of the blood meal (Hien, 1976a). In general, it appears that there is a linear correlation between blood meal size and number of eggs oviposited. Hien (1976a) observed that, on average, *Ae. albopictus* females lay eggs after a blood meal of at least 0.7 mg. For females taking from 0.8 mg to 2.5 mg of blood, the average number of eggs produced in the first gonotrophic cycle was 72 per female (Hien, 1976a). The study

also demonstrated that the number of eggs produced increased with the size of the blood meal taken by the female (85 or more eggs at 2.0 mg of blood).

A study conducted by Klowden and Chambers (1992) showed that *Ae. albopictus* females possess the ability to utilize extremely small blood meals to develop their eggs, in contrast to other species of *Stegomyia* (i.e., *Ae. aegypti*). Values as low as 0.1 µl of blood were enough to trigger egg development in *Ae. albopictus* strains from Lake Charles, Louisiana. The average number of eggs oviposited was 18 per female. In contrast, the other North American *Stegomyia, Ae. aegypti,* was unable to develop any eggs unless the blood meal volume was more than 1 µl. Gubler and Bhattacharya (1971) found that the mean number of eggs in the first gonotrophic cycle was 63.4 per female. Similar results were obtained in two other studies: Udaka (1959) reported 62 eggs per female feeding on sugar and blood, and Sockiman et al. (1984) observed an average of 57.5 eggs per female after a single blood feeding.

Based on measurements of parity rates for *Ae. albopictus*, Hawley (1988) determined that the number of egg batches laid by a female wild mosquito in its life-span is in the range of 0.2 to 2.1. The average number of ovipositions inferable from these data is approximately one.

The number of eggs laid also depends on the physiological age of the female, and the number progressively decreases as age increases (Gubler and Bhattacharya, 1971; Hien, 1976a). Generally speaking, the first gonotrophic cycle produces the highest number of eggs, with a gradual decrease in subsequent cycles. On average, *Ae. albopictus* females in the laboratory were found to produce 283–344 eggs per mosquito during their life cycle (Gubler and Bhattacharya, 1971; Hien, 1976a).

Autogeny has been observed in laboratory strains of *Ae. albopictus* (Bat-Miriam and Craig, 1966; Cui, 1982; Klowden and Chambers, 1992). Autogeny in this case is defined as egg maturation without an exogenous source of protein, namely, the blood meal. Conversely, a species requiring ingestion of proteinaceous foodstuffs for egg development is known as an anautogenous species (Roubaud, 1929). It has been suggested that autogenous mosquitoes accumulate considerably more reserves during their larval life than do anautogenous ones. This situation may be related to the somewhat longer larval developmental periods in autogenous strains. Autogeny in mosquitoes is not controlled solely by larval nutritional conditions but also by genetic components (Twohy and Rozeboom, 1957). Autogeny therefore has ecological significance, since it allows the mosquito to lay eggs even in the absence of a host for feeding, thus ensuring the continuity of the species.

In *Ae. albopictus* strains from Lake Charles, Louisiana, autogenous behavior was expressed in adult females maintained on a sugar diet (Klowden and Chambers, 1992). In a sample of 100 individuals, 5% displayed autogeny. No data on the number of eggs oviposited per female are provided by the researchers. Based on data from this research, it was hypothesized that food reserves accumulated in an extended larval life cycle, as compared to that of *Ae. aegypti*, may favor stores of lipids and proteins that enhance the expression of autogeny in *Ae. albopictus*. These observations were part of studies assessing the reproductive and metabolic differences between North American strains of *Ae. albopictus* and *Ae. aegypti*.

With strains from Mauritius and Madagascar, Bat-Miriam and Craig (1966) demonstrated that adults that were fed only on sugar and raisins produced a few eggs. The strain from Mauritius was able to present autogeny for 12 generations. Cui (1982) observed that larvae collected in Guangzhou City and reared in the laboratory displayed autogeny. The autogeny index reported for the Guangzhou strain varied from 1.96 to 2.96, while in the Mauritius strain it was 2.7 eggs per female.

Oviposition activity and horizontal and vertical ecological stratification have been studied by Gubler (1971b). He determined from a series of 18 ovitrap collections that most of the eggs were laid at ground level, but some were deposited at a height of 15 meters, in the tops of trees in Calcutta, India. In Paradeniya, Sri Lanka, Amerasinghe and Alagoda (1984) made similar observations: *Ae. albopictus* females laid about 52% of their eggs at ground level, and there was a decrease in oviposition with increasing height above ground. Only 33% of the eggs were laid at 3.5 meters and just 16% of the eggs were laid at 7 meters. The results suggest that *Ae. albopictus* females, although preferring horizontal range stratification for oviposition, are able to migrate and oviposit in the treetops.

Oviposition sites are affected by habitat type, light, temperature, and humidity, as well as by such subtle influences as characteristics of the water (biotic and abiotic) and even the oviposition surface (Bently et al., 1976; Amerasinghe and Alagoda, 1984). Ho et al. (1972) reported that, under laboratory conditions, female *Ae. albopictus* preferred to oviposit in habitats with a rough gray surface and low reflectivity rather than on a smooth black surface with high reflectivity. Yap (1975) observed that ovitraps coated with red and black were preferred over ovitraps of other colors. In their natural habitat, *Ae. albopictus* usually lay eggs in water reservoirs containing decaying vegetable matter (Hien, 1976a).

The quality of larval food appears to affect the adult's oviposition capacity. This effect was observed in *Ae. albopictus* females reared with banana powder in the larval stage: egg laying was particularly weak except at a constant temperature (Ho et al., 1972).

In nature, it was observed that *Ae. albopictus* females seldom laid all of their mature eggs in a single oviposition. Instead, they appeared to move from place to place, at each site leaving behind a few eggs. The female probably lays all mature eggs during the course of several ovipositions, periodically interrupting her egg laying to fly to another

container. This strategy is considered a species survival mechanism (Rozeboom et al., 1973).

Laboratory observations assessing the influence of blood sources in oviposition have been carried out in New Orleans, Louisiana. The results showed that mosquitoes feeding on rodent species laid significantly more eggs than those feeding on avian, rabbit, or human hosts (NOMCB, 1989).

Host Preference

Aedes albopictus females feed on a wide range of mammals as well as birds. Host-feeding patterns for wild *Ae. albopictus* populations in the New World showed that the species is an opportunistic feeder that appears to be primarily attracted to mammals rather than other types of hosts (Savage et al., 1993). Savage and co-workers conducted studies in the summers of 1989 and 1990 in a large tire dump located in Potosi, Missouri. Their sample consisted of 172 *Ae. albopictus* females, which were tested by means of the precipitin test and direct ELISA. The results showed that 64% of the mosquitoes had fed on mammals and 16.9% on birds. This study identified nine mammalian taxa as hosts: rabbits, deer, and dogs (the three most common), followed in decreasing order by humans, squirrels, opossums, myomorphs (except *Rattus*), bovines, and raccoons. Four avian taxa were also identified as *Ae. albopictus* blood hosts: passeriforms, columbiforms, ciconiiforms, and quail. Various blood meals came from unidentified mammalian and avian hosts.

In an extension of the Missouri studies to four more states (Florida, Illinois, Louisiana, and Indiana), Niebylski (1992) and Niebylski et al. (1994a) found two more mammalian taxa (rats and cats), as well as turtles, as preferred hosts, in addition to the nine mammalian taxa named above. The variation in blood hosts between sites and within sites could be governed by the relative abundance of specific vertebrates at the time of sampling.

In Thailand and the Hawaiian Islands, *Ae. albopictus* females collected in a sylvan environment fed on humans, horses, pigs, buffalo, bovine species, dogs, chickens, and boobies (Tempelis et al., 1970; Sullivan et al., 1971). In the Hawaiian Islands, 93% of the females fed on mammals and 7% on birds.

Under laboratory conditions, *Ae. albopictus* feeds on humans, rabbits, mice, chickens, rats, and guinea pigs (Del Rosario, 1963; Ho et al., 1972). *Ae. albopictus* females in breeding cages have also been reported to feed on snakes and frogs (Miyagi, 1972).

According to Ho et al. (1972), *Ae. albopictus* prefers to feed on humans, but host availability appears to play a fundamental role in the average behavior of the mosquito populations. The confirmation in the U.S. studies that *Ae. albopictus* is an opportunistic blood feeder supports the findings of other researchers (Tempelis et al., 1970) and adds to the potential of the species to become involved in the enzootic/endemic transmission cycles of indigenous arboviroses and other vector-borne diseases. *Ae. albopictus* breeds in areas surrounding the human environment and has demonstrated highly anthropophilic behavior; thus, the species can participate in the sylvan zoonotic cycle and carry diseases to man.

Biting Behavior

On average, *Ae. albopictus* females take their first blood meal two days after emergence (Del Rosario, 1963; Hien, 1976a). Adult females are vigorous daytime biters (although they sometimes bite at night) and typically bite outdoors (Feng, 1938; Sheng and Wu, 1951; Surtees, 1966; Ho et al., 1972; Pant et al., 1973; J. Freier, unpublished information). The diurnal biting cycle of *Ae. albopictus* appears to be generally bimodal, with one period in early morning and the other in evening (Gubler, 1971b; Ho et al., 1973; Basio and Santos-Basio, 1974).

Diel studies conducted during the summer of 1987 on *Ae. albopictus* strains from New Orleans, Louisiana, showed this bimodal cycle of biting activity. The first biting cycle occurred between 6:00 and 10:00 a.m. and the second between 4:00 and 10:00 p.m. Statistical analysis suggested a positive correlation between biting activity and relative humidity ($r = 0.33$, $p < 0.005$). The same study observed biting activity throughout the 24-hour period, decreasing but not disappearing during the night-time hours (NOMCB, 1987).

In Calcutta, Gubler (1971b) observed that the diurnal activity of *Ae. albopictus* females presented a primary peak between 6:00 and 8:00 a.m. and a secondary peak between 4:00 and 6:00 p.m. In Singapore, well-defined biting activity of female *Ae. albopictus* was found, with a morning peak just after sunrise at 7:30 a.m. and an evening peak around sunset from 5:30 to 6:30 p.m. The prominent evening peak may be an important factor contributing to disease transmission, since in certain tropical areas human outdoor activity increases in late afternoon (Ho et al., 1973).

In the Philippines, Basio and Santos-Basio (1974) observed a minor biting peak between 9:00 and 10:00 a.m. and a major peak between 4:00 and 5:00 p.m. The biting cycle was similar in four different geographical areas.

Although biting activity of females occurred predominantly at ground level, it was observed as high as 9 meters above the ground during the peak biting time in Calcutta (Gubler, 1971b). Population studies of *Ae. albopictus* conducted by Mogi and Yamanura (1981) indicate that *Ae. albopictus* attraction to humans depends on host factors such as sex, age, race, and clothing, as well as mosquito responsiveness as influenced by circadian rhythm, microclimatic conditions, and undetermined factors related to the individual host. Thus, females attack humans under the

guidance of carbon dioxide, moisture, organic chemicals, and visual factors including movement. The same study found that the range of attraction of *Ae. albopictus* to a human is a circle with a radius of about 4–5 meters (an area of 50–80 m^2). The host-seeking pattern of *Ae. albopictus* appears to follow two phases: an initial random flight and a directional flight after encountering stimuli from a host. This assertion is supported by the observation that *Ae. albopictus* distribute vertically within the range where stimuli from a human being on the ground are detectable.

Seasonal abundance of adults varies according to the geographical area. Therefore, seasonal biting activity is influenced mainly by temperature and rainfall.

In New Orleans, adult mosquito abundance peaks seven days after the beginning of rainfall. Larval mosquito populations reach their peak densities in tree holes and tires during the month of June. Adults are found between the months of May and August. Most adult activity disappears in late September following the onset of diapause (NOMCB, 1987; NOMCB, 1988).

In the tropics, for example, in the city of Singapore, there are three adult population peaks: in March, in June–July, and in November–December. Thus, female feeding activity is highest during those three periods. The population peaks closely follow those of rainfall (Ho et al., 1971).

On the subtropical island of Okinawa, Toma et al. (1982) found females feeding throughout the year, with peaks in feeding activity occurring from April to June and from August to November. In temperate areas of Japan, adult peaks occur from late March to mid-September. La Casse and Yamaguti (1950), in Honshu, Japan, observed that biting rates of *Ae. albopictus* peaked during the last two weeks of August.

Flight Range

Bonnet and Worchester (1946) determined during mark-release-recapture studies with *Ae. albopictus* that the maximum recapture distance was 134 meters. Thus, it is apparent that *Ae. albopictus* has a short flight range, rarely reaching 500 meters (Stojanovich and Scott, 1965). This observation has been confirmed by recent dispersal studies conducted with North American *Ae. albopictus* strains from Potosi, Missouri (Niebylski, 1992; Niebylski et al., 1994b). Using mark-release-recapture trials, the maximum dispersal distance estimated for females was 525 meters, whereas the maximum dispersal distance for males was 225 meters. It was also noted that more than 90% of the *Ae. albopictus* specimens from the study area dispersed less than 100 meters.

Resting Behavior

Aedes albopictus adults have been found resting outdoors in clearings and rubber plantations in Malaysia. In China, the adults appeared in mosquito nets, kitchens, drawing rooms, pig sties, or among weeds in the field (Surtees, 1966; Ho et al., 1972).

In the United States resting *Ae. albopictus* have been found in forest fringes where both canopy and understory are present (Niebylski, 1992).

Adult Morphology

Adults of the genus *Aedes* can be differentiated from other Culicidae because their abdomen is pointed. The main characteristic that distinguishes *Ae. albopictus* from *Ae. aegypti* is the conspicuous lyre-shaped silver pattern on the scutum of *Ae. aegypti,* compared with the distinct longitudinal silver line of *Ae. albopictus.* If the scales from the thorax are inadvertently rubbed off during collection or if other handling problems occur, there is another character that can distinguish these species. The clypeus, a structure located on the head between the palpi, is covered with white scales in the *Ae. aegypti* female and black scales in the *Ae. albopictus* female. A pictorial key provided by Dr. G. O'Meara and another one from the Superintendencia de Campanhas de Saúde Pública (SUCAM, 1989) in Brazil (Figures 15 and 16) show differences in greater detail for the adult stages of both species. In addition, a Walter Reed Biosystematics Unit plate illustrates the external morphology of adult *Ae. albopictus* (Figure 17).

Competition Studies

Aedes albopictus utilizes the same kind of artificial water containers that are the principal sources of *Ae. aegypti*, and several studies report that *Ae. albopictus* and *Ae. aegypti* may share the same habitat (Gilotra et al., 1967; Chan, K. L., et al., 1971; Ho et al., 1972; Azzizar, 1980; Sprenger and Wuithiranyagool, 1986; Nasci et al., 1989; O'Meara et al., 1993). Because of this association, it has been hypothesized that in some parts of Southeast Asia *Ae. aegypti* has completely replaced the indigenous *Ae. albopictus* in urban areas (Pant et al., 1973). Conversely, observations on the spread of *Ae. albopictus* in the southern coastal states of the United States indicate that the expansion appears to be occurring at the expense of *Ae. aegypti.* The introduction of *Ae. albopictus* has been accompanied by a drastic and rapid decline of *Ae. aegypti* populations (Nasci et al., 1989; O'Meara et al., 1993).

Historically, laboratory studies of larval competition conducted with different Asian strains of *Ae. albopictus* and *Ae. aegypti* showed *Aedes aegypti* better able to compete than *Ae. albopictus* (Macdonald, 1956; Gilotra et al., 1967; Moore and Fisher, 1969; Sucharit et al., 1978). Information obtained by these researchers suggested that *Ae. albopictus* would not become established in locales inhabited by *Ae.*

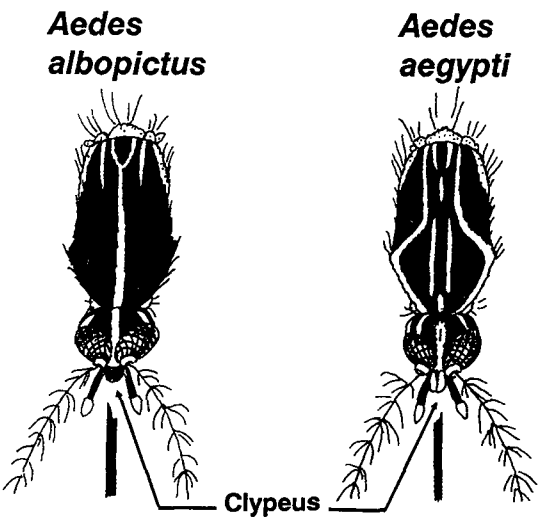


Figure 15. Differences in the clypeus of *Ae. albopictus* and *Ae. aegypti*. The female *Ae. albopictus* clypeus is covered only with dark scales, while *Ae. aegypti* shows white scales. (Drawings provided by Dr. George O'Meara, Medical Entomology Laboratory, University of Florida at Vero Beach.)

aegypti because of competitive displacement or competitive exclusion.[4]

The phenomenon of competitive displacement involving *Ae. albopictus* and other species has also been suggested by other scientists. For instance, in cage experiments Gubler (1970b) demonstrated induced sterility when males of *Ae. albopictus* cross-inseminated females of *Ae. polynesiensis*. Gubler (1970c) suggested a competitive displacement principle by showing experimentally that at a ratio of 10 *Ae. albopictus* males to 1 *Ae. polynesiensis* male, a cage colony of *Ae. polynesiensis* was completely eradicated.

Likewise, *Ae. albopictus* is reported to have displaced *Ae. guamensis* from some areas of Guam and the Mariana Islands. *Ae. guamensis* is indigenous to Guam, but *Ae. albopictus* is known to have been introduced in 1944. One study hypothesized that (in part due to competition) the population density of *Ae. guamensis* decreased by as much as 95% in artificial containers and by 30% in natural habitats, while that of *Ae. albopictus* increased (Rozeboom and Bridges, 1972).

In North America, *Ae. albopictus* has been found associated with *Ae. triseriatus* in tires and tree holes (NOMCB, 1987; Livdahl and Willey, 1991; O'Meara et al., 1993). Laboratory larval competition studies between the two species using tree hole and tire fluid suggest that they could coexist in tree holes, but that *Ae. triseriatus* would become locally extinct in tire habitats (Livdahl and Willey, 1991). The mechanism proposed by the researchers to explain this result is that "resources exist within tires that can be used more effectively by *Ae. albopictus* than *Ae. triseriatus*, and that tree hole fluid contains resources that each species exploits differentially." In general, these laboratory-based assumptions have been supported by field studies conducted in Florida which showed a "progressive increase in the frequency of artificial containers with *Ae. albopictus* and a concomitant decrease in those with *Ae. triseriatus*" (O'Meara et al., 1993).

The apparent success of *Ae. albopictus* as a competitor seems to be corroborated by observations on the relative abundance of the other New World *Stegomyia*, *Ae. aegypti*,

[4]The competitive exclusion principle, or Gause's hypothesis, is the principle that two species having identical ecological requirements cannot coexist indefinitely.

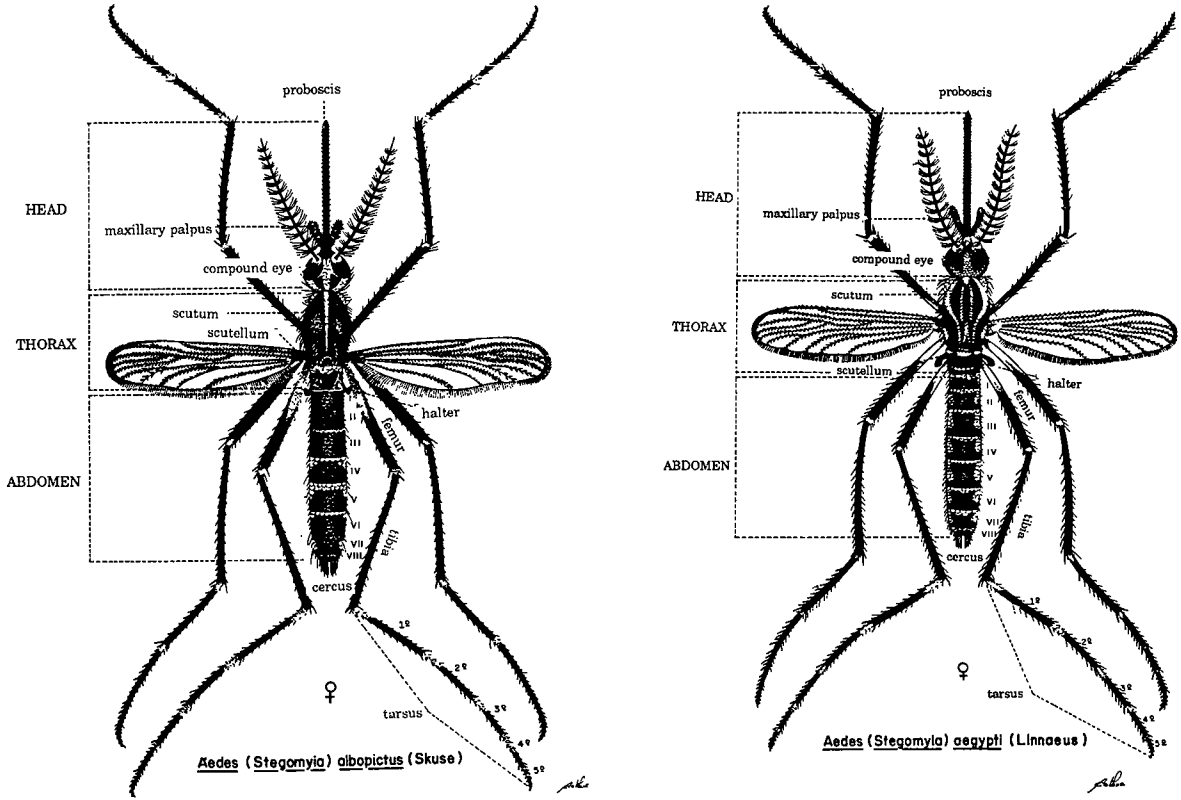


Figure 16. Morphological characteristics of *Ae. albopictus* and *Ae. aegypti* adult females. *Aedes albopictus*, left, shows a distinct longitudinal silver line on the scutum, while *Aedes aegypti*, right, has a conspicuous lyre-shaped silver pattern. (Drawings by Arthur Botelho de Barros, Superintendencia da Campanhas de Saúde Pública, Brazil.)

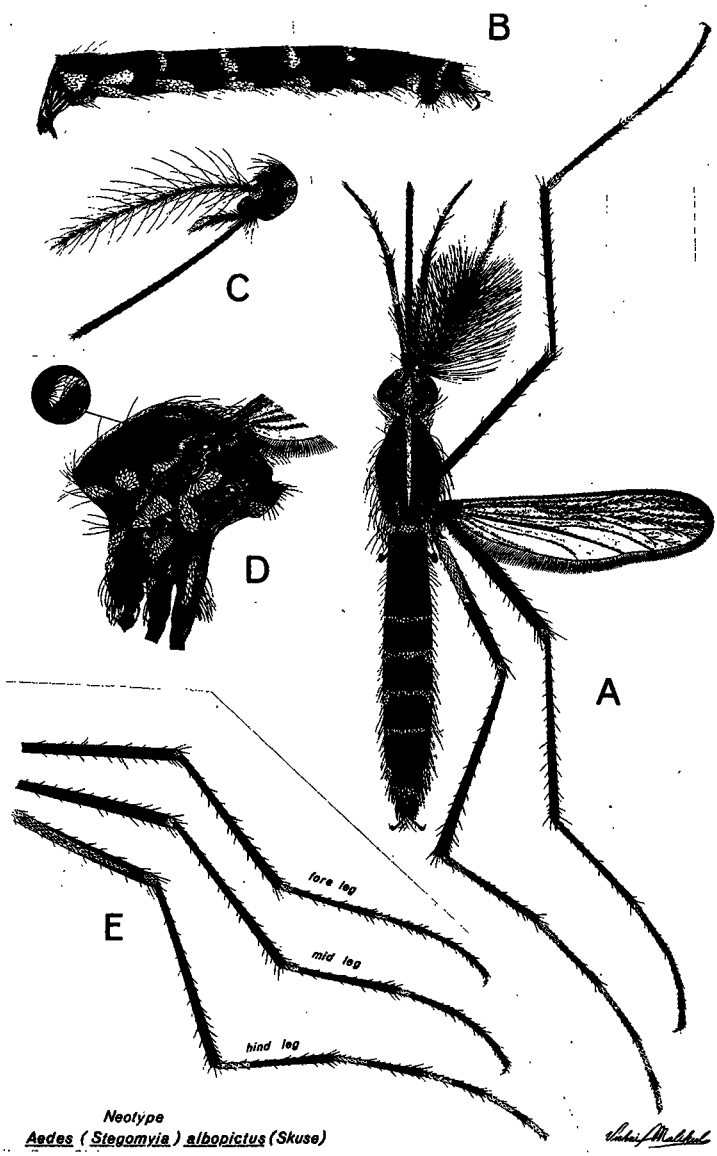


Figure 17. Adult morphology of *Ae. albopictus*. A, dorsal aspect of the male; B, lateral aspect of the male abdomen; C, lateral aspect of the female head; D, lateral aspect of the male thorax; E, anterior surface of the male legs. (Drawings provided by Walter Reed Biosystematics Unit, Smithsonian Institution, Washington, D.C.)

in various southern cities of the United States in the 1980s, and the subsequent dramatic decrease in *Ae. aegypti* populations following the introduction of *Ae. albopictus*. Field observations of artificial habitats, including tires, in Texas, Alabama, and Florida appear to reconfirm the phenomenon (Sprenger and Wuithiranyagool, 1986; Hobbes et al., 1991; O'Meara et al., 1993).

Another hypothetical mechanism suggested for competitive replacement of *Ae. aegypti* by *Ae. albopictus* in North America is parasitism. For instance, the intestinal gregarine protozoan *Ascogregarina taiwanensis*, which parasitizes *Ae. albopictus* larvae, appears to have come to the New World along with *Ae. albopictus* (Munstermann and Wesson, 1990). After spores are ingested by the larvae, the sporozoites penetrate and grow in the midgut cells, then emerge and go to the Malphigian tubes where their life cycle is completed by sexual fusion of the gametes, cyst production, and spore excretion by the emerged adults. *Ae. albopictus* tolerates its parasite well; very heavy infections produce a maximum larval mortality rate of 10%–20%. Experiments carried out by G. Craig at the University of Notre Dame have demonstrated cross-infections of *Asc. taiwanensis* in *Ae. aegypti*. However, in that species the infection settles in the midgut and does not complete its sexual cycle. More important, heavy infections of *Asc. taiwanensis* have been shown to produce high larval mortality in *Ae. aegypti*. Thus, it has been suggested that *Ae. albopictus'* parasite gives it a major competitive edge in the field, which in turn may help to explain the decrease in *Ae. aegypti* populations.

Edgerly et al. (1993) studied the inhibitory effects of larvae on the hatch rate of conspecific and congeneric eggs as a potential population regulatory mechanism. Their laboratory experiments assessed the egg hatch rates of *Ae. albopictus* in response to increases in the larval density of two possible competitors, *Ae. aegypti* and *Ae. triseriatus*. The rationale behind the research approach is that after egg flooding, "microorganisms colonize the egg surfaces and the subsequent decline in dissolved oxygen due to microbial respiration triggers hatch." Therefore, larval feeding on microorganisms could be a simple mechanism for hatch inhibition. "Foraging larvae of other *Aedes* species may impose interspecific, as well as intraspecific, hatch inhibition." Eggs of each species were exposed to varying combinations of larval species and density for 24 hours and their respective hatch rates were then assessed. Of the three species, *Aedes albopictus* eggs showed the lowest level of inhibition when exposed to high larval densities. In addition, at the lowest larval density, *Ae. albopictus* imposed the most intense interspecific hatch inhibition. It was hypothesized that the observed differential hatch responses are the result of differences in larval feeding rates, respiration rates, and oxygen thresholds required for hatch, as well as differential changes in larval grazing behavior with increased density. The conclusions of the study suggest that the relative success of "*Ae. albopictus* in inhibiting egg hatch of *Ae. triseriatus* and *Ae. aegypti*, combined with their propensity to hatch into occupied habitats, may provide the species with a significant advantage as they encounter resident populations." Edgerly and co-workers (1993) concluded that the "competitive ability of *Ae. albopictus* larvae may help to explain why *Ae. albopictus* has achieved rapid dominance in domestic container habitats previously occupied by *Ae. triseriatus* and *Ae. aegypti* in the southern United States."

Further studies focusing on adult mating behavior have examined mating interference (interspecific matings) to try to explain the observed differences between *Ae. albopictus* and *Ae. aegypti*. Interspecific matings between *Ae. albopictus* males and *Ae. aegypti* females have been demonstrated in both field and laboratory experiments (Nasci et al., 1989). *Ae. aegypti* females inseminated by *Ae. albopictus* males contained clumps of a few dead sperm in their spermatheca, which implies refractoriness to further mating by the female. In turn, the observations suggest mating interference at high *Ae. albopictus* densities, which may be an important factor in determining the distribution of the two *Stegomyia* in North America. The problem with this likely explanation is that the experiments have not been replicated either in cages or in the field by other researchers.

Additional approaches have been pursued to try to explain the decline of *Ae. aegypti* and the role *Ae. albopictus* has played in that decline in North America, but a conclusive general explanation has not yet emerged. More field studies are needed to assess the true impact of *Ae. albopictus* on *Ae. aegypti* populations. In general, researchers agree that not enough evidence is available to prove whether the decline of *Ae. aegypti* and *Ae. triseriatus* has been caused by *Ae. albopictus*. In all likelihood, a combination of several factors (including larval competition) may be contributing to the decline of *Ae. aegypti* and other *Aedes* in North America.

Regarding the Asian situation, in which *Ae. aegypti* appears to have displaced *Ae. albopictus*, Edgerly et al. (1993), in agreement with Hawley (1988), consider that "habitat changes can have dramatic effects on the outcome of biological invasions; rampant urbanization in Southeast Asia apparently stimulated an increase in abundance in *Ae. aegypti* introduced from Africa, at the expense of native *Ae. albopictus*."

Despite several likely explanations, both phenomena—the Asian and North American competitive *Aedes* replacements—still constitute an ecological enigma.

DISEASE RELATIONSHIPS

The potential public health importance of *Ae. albopictus* is indicated by its ability to transmit various arboviruses, filarial worms, and protozoa. Both field and laboratory stud-

ies indicate that this species is susceptible to infection with and able to transmit numerous pathogens of medical importance. However, it is important to note that thus far *Ae. albopictus* has not been implicated in the transmission of diseases of public health importance in the Americas. General information on arboviral diseases and an overview of some of the more important of these diseases, as well as their potential relationship to *Ae. albopictus*, are presented below.

General Information on Arboviral Diseases

Arthropod-borne viruses (arboviruses) consist of a group of animal viruses that are able to reproduce in an arthropod and can be transmitted to a vertebrate host. According to the World Health Organization (1985), "arboviruses are viruses that are maintained in nature principally, or to an important extent, through biological transmission between susceptible vertebrate hosts by hematophagous arthropods or through transovarial and possibly venereal transmission in arthropods; the viruses multiply and produce viraemia in the vertebrates, multiply in the tissues of arthropods, and are passed on to new vertebrates by the bites of arthropods after a period of extrinsic incubation." Vertical (transovarial) and venereal transmission in arthropods may serve as basic long-term maintenance mechanisms for some arboviruses.

DeFoliart et al. (1987) consider vertical transmission to be a survival mechanism developed by the virus to resist adverse climatic conditions that may affect its arthropod host. Vertical transmission involves "the direct transfer of infection from a parent organism to his, her, or its offspring." In contrast, horizontal biological transmission involves ingestion of the virus in the blood of a viremic vertebrate, multiplication of the virus in the midgut of the mosquito, dissemination of the virus to the hemocoel, infection of the salivary glands, and transmission of the virus to a susceptible vertebrate host by bite (Turell, 1988). The virus can also be transmitted either horizontally by arthropods infected vertically, or mechanically by arthropods that obtain a partial blood meal from an infected host and then continue their feeding on a susceptible one (i.e., arthropods can serve as contaminated flying syringes).

Shroyer (1986) and Mitchell (1991) reviewed the vector competence of *Ae. albopictus*, including North and South American strains, to arbovirus infections. The term "vector competence" as used herein corresponds to the definition cited by Mitchell (1983): "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." Laboratory studies have demonstrated that *Ae. albopictus* is a competent vector of most of the American encephalitis viruses. These include members of the family Togaviridae, genus *Alphavirus* (eastern equine encephalitis [EEE], western equine encephalitis [WEE], Venezuelan equine encephalitis [VEE], and Mayaro [MAY] viruses); the family Flaviviridae, genus *Flavivirus* (St. Louis encephalitis [SLE], yellow fever, and dengue viruses); and the family Bunyaviridae, genus *Bunyavirus* (La Crosse encephalitis [LAC], trivittatus [TVT], and Jamestown Canyon [JC] viruses). Table 1 summarizes the key vector competence information available for *Ae. albopictus* in studies carried out primarily with strains from the Americas. It also includes some relevant information from studies conducted with strains from Hawaii or Asia that predated the discovery of *Ae. albopictus* in the New World. *Aedes albopictus* has been shown to be susceptible to infection with at least 26 different arboviruses and able to transmit at least 24 of them. Information on natural and experimental infections of *Ae. albopictus* and its potential to transmit these viruses to humans and other vertebrates is discussed below.

Arbovirus Field Isolations in the Americas

Four arboviruses have been isolated from *Ae. albopictus* collected at various locations in the continental United States. These are Potosi (POT) virus from mosquitoes collected in central Missouri in 1989, Tensaw (TEN) virus from Texas in 1991, Keystone (KEY) virus from central Florida in 1991, and EEE virus from central Florida in 1991. The role of *Ae. albopictus* in the natural transmission cycles of these four viruses remains obscure. Of the four isolations, probably the most disturbing one is that of EEE virus (Mitchell et al., 1992).

Eastern Equine Encephalitis (EEE)

This RNA virus, belonging to the genus *Alphavirus* of the family Togaviridae, forms part of a complex of encephalitides transmitted by mosquito species (Acha and Szyfres, 1987). In North America the virus is maintained in freshwater swamp habitats in an enzootic cycle principally involving *Culiseta melanura* and a variety of bird species (Scott and Weaver, 1989). Various species of mosquitoes are believed to be bridge vectors between this maintenance cycle and susceptible mammalian hosts. In North America, these vectors include *Coquillettidia perturbans* and *Aedes sollicitans*; in the tropical countries of the Americas, the vectors appear to be *Culex nigripalpus*, *Culex taeniopus*, and *Aedes taeniorhynchus* (Calisher et al., 1981).

EEE is an uncommon but severe disease of humans in the Americas with an overall case-fatality rate among clinical cases of between 50% and 80% (Shope, 1985a). The disease in humans has a sudden onset and is manifested by high fever, cephalalgia, conjunctivitis, nausea, vomiting, and lethargy, progressing rapidly to delirium and coma. Neurologic signs include neck stiffness, convulsions, spasms of the muscles of the extremities, and altered re-

flexes. A biphasic course is common in children, with fever, vomiting, and headaches for one or two days, followed first by an apparent recovery and then by a rapidly fatal encephalitis. Sequelae are common and more severe in the young. About 60% of the survivors show mental retardation (Shope, 1985a; Acha and Szyfres, 1987). Sporadic human cases of EEE have been reported from Brazil, the Dominican Republic, Jamaica, and Trinidad and Tobago. (WHO, 1985). Elsewhere in the Americas, the virus has been isolated in Argentina, Canada, Colombia, Cuba, Guatemala, Guyana, Haiti, Mexico, Panama, Peru, the United States, and Venezuela (Acha and Szyfres, 1987).

Although EEE can cause severe disease in humans, it primarily affects domestic mammals and exotic birds. Numerous epizootics have been reported among horses, with high mortality rates. Such outbreaks may or may not be accompanied by clinical cases in the human population. Exotic birds that can be affected by EEE include pheasants,

Table 1. Susceptibility of *Ae. albopictus* to oral infection with arboviruses, ability to transmit them by bite, and status in nature.

Virus	Oral infect.	Oral trans.	Infected in nature	References
Chikungunya[a,b]	+	+	No	Tesh et al., 1976; Turell et al., 1992b
Dengue 1,2,3,4[a,b]	+	+	Yes	Rosen et al., 1985; Mitchell et al., 1987
EEE[b]	+	+	Yes	Mitchell et al., 1992; Turell et al., 1994
Jamestown Canyon[b]	+	+	No	Grimstad et al., 1989
JE[b]	+	+	Yes	Rosen et al., 1978
Keystone[b]	+	?	Yes	Mitchell et al., 1992
La Crosse[b]	+	+	No	Streit and Grimstad, 1990
Mayaro[b]	+	+	No	Smith and Francy, 1991
Nodamura[a]	+	?	No	Tesh, 1980
Oropouche[b]	+	−	No	Smith and Francy, 1991
Orungo[a]	+	+	No	Kay et al., 1982; Tomori and Aitken, cited in Shroyer, 1986
Potosi[b]	+	+	Yes	Francy et al., 1990a
Rift Valley fever[b]	+	+	No	Turell et al., 1988
Ross River[a,b]	+	+	No	Mitchell and Gubler, 1987; Mitchell et al., 1987
Sindbis[b]	+	+	No	Dohm and Turell, unpublished data, 1993
San Angelo[b]	+	+	No	Tesh, 1980
SLE[a]	+	+	No	Mitamura et al., 1940, cited in Shroyer, 1986; Hardy et al., 1980
Tensaw[b]	?	?	Yes	Mitchell et al., 1992
Trivittatus[b]	+	-	No	Grimstad et al., 1989
West Nile[b]	+	+	No	Akhter et al., 1982
WEE[b]	+	+	No	Kramer et al., unpublished information, cited in Mitchell, 1991; Simmons et al., cited in Shroyer, 1986
VEE IAB[b]	+	+	No	Turell et al., 1992a
Yellow fever[a,b]	+	+	No	Mitchell et al., 1987; Miller and Ballinger, 1988

[a] Studies conducted with *Ae. albopictus* strains from Hawaii and/or Asia.

[b] Studies conducted with *Ae. albopictus* strains from mainland United States and/or Brazil.

EEE = Eastern equine encephalitis virus

JE = Japanese encephalitis virus

SLE = St. Louis encephalitis virus

WEE = Western equine encephalitis virus

VEE = Venezuelan equine encephalitis virus

Source: Data taken from Shroyer (1986), Mitchell (1991), and updated information published as of July 1993. Special emphasis is given to studies carried out with strains from the Americas.

quails, peking ducks, emus, and partridges. In some outbreaks in the United States attack rates of up to 50% have been recorded, producing serious economic losses (WHO, 1985).

Fourteen strains of EEE virus were isolated from *Ae. albopictus* collected during the summer of 1991 in a tire dump in Polk County, Florida (Mitchell et al., 1992). This was the first reported isolation of an arbovirus of known public health importance from wild-caught *Ae. albopictus* in the United States. In June 1992, after active participation by the local Mosquito Abatement District and destruction and removal of the tire dump, several research agencies failed to recover EEE virus from *Ae. albopictus* pools from the same area.

Several studies have examined the potential for *Ae. albopictus* to transmit EEE virus. A strain of *Ae. albopictus* from Houston, Texas, was shown to be highly susceptible to infection after feeding on a viremic chick; 100% (n = 10) and 40% (n = 20) transmitted virus by bite (Scott et al., 1990). Turell et al. (1994) examined mosquitoes from the tire pile in Polk County, Florida, for their susceptibility to a strain of EEE virus recovered from *Ae. albopictus*. Again, these mosquitoes were highly susceptible to oral infection [98% (n = 360)], and 40% (n = 216) transmitted virus by bite. These *Ae. albopictus* were significantly more susceptible to infection with EEE virus than were *Ae. sollicitans* or *Ae. taeniorhynchus*, known bridge vectors of EEE virus (Turell, unpublished data). Although neither Scott et al. (1990) nor Turell et al. (1994) observed any evidence of vertical transmission (2,952 progeny examined), transovarial transmission may still play a role in the long-term maintenance of this virus in nature. To date, the public health significance of the EEE field isolations from *Ae. albopictus* remains unclear. However, because of the high sensitivity of this species to EEE viral infection, its opportunistic feeding behavior, and its continued expansion within the Americas, the natural transmission cycles of EEE virus may be modified by the inclusion of *Ae. albopictus*.

Potosi (POT)

Ten strains of POT, a newly recognized virus, were recovered from *Ae. albopictus* collected in the summer of 1989 in the United States (Francy et al., 1990a). The isolates were determined to belong to the family Bunyaviridae, genus *Bunyavirus*, and the Bunyamwera serogroup. These isolations were made from pools of *Ae. albopictus* captured in Potosi, Missouri; the minimal field infection rate in September 1989 was 8.9 per 1,000 mosquitoes. Six additional isolations from the same area were made during the same collecting period (Mitchell et al., 1990). Attempts to isolate additional strains during the summers of 1990 and 1991 were unsuccessful.

Studies of vertebrate susceptibility to POT virus were carried out with suckling mice, hamsters, rabbits, and pigeons. This virus is pathogenic for suckling mice, as 85% (n = 59) became symptomatic after intracerebral inoculation of POT virus (Niebylski, 1992). The range of symptoms detected in mice included loss of coordination, tremor and prostration, and limb paralysis. Overall mortality was 62%, with an average survival time of 8.8 days. Hamsters and rabbits developed low levels of viremia (2.0 $\log_{10}$ median tissue culture infective doses [$TCID_{50}$]/ml to 4.3 $\log_{10}$ $TCID_{50}$/ml of whole blood) with no sign of illness. Neither viremia nor signs of illness were detected in pigeons inoculated with POT virus (Niebylski, 1992). Transmission studies indicate that *Ae. albopictus* can transmit POT virus horizontally (Heard et al., 1991; Mitchell et al., 1990) but not vertically (Francy et al., 1990a). Preliminary testing of people working at the sampling sites demonstrated the presence of neutralizing antibody to the new virus in one individual. However, the public health threat posed by POT virus has not been fully resolved, and additional information on human pathology is needed.

Tensaw (TEN) and Keystone (KEY)

TEN virus was isolated from a pool of 38 *Ae. albopictus* collected on 25 July 1991 in Montgomery County, Texas (Mitchell et al., 1992). This virus belongs to the family Bunyaviridae, genus *Bunyavirus*, and was isolated for the first time in 1960, from *Anopheles crucians* collected in Baldwin County, Alabama (Coleman, 1969). The virus produces clinical disease and death in suckling and adult mice but not in rabbits, guinea pigs, or hamsters. Antibodies have been detected in dogs, raccoons, cattle, and humans (Chamberlain et al., 1969). The importance of TEN virus as a public health threat remains unknown (Coleman, 1969).

KEY virus was recovered from a pool of *Ae. albopictus* collected during the same Florida studies that recovered EEE virus from this species. The virus belongs to the family Bunyaviridae, genus *Bunyavirus*, and has been isolated from cotton rats (*Sigmodon hispidus*) in Georgia and Florida (Sudia et al., 1971a). *Aedes atlanticus* and/or *tormentor* appears to be the principal vector, although KEY virus has been isolated from nine other mosquito species. Antibodies have been detected in rice rats, cottontail rabbits, gray squirrels, raccoons, white-tailed deer, sika deer, horses, and humans (Sudia et al., 1971a; Watts et al., 1982).

Although the impact of TEN and KEY viruses on human health remains unknown, the isolation of these viruses from *Ae. albopictus* and its ability to transmit them raises the important question of how the presence of a new vector may affect natural transmission cycles. As stated by Francy et al. (1990a), "the possibility remains that other viruses, which heretofore have not infected humans to any appreciable degree because of nonhuman feeding habits of their

arthropods vectors, may be transmitted to humans by *Ae. albopictus* as a result of the aggressive feeding of this species on humans as well as on other mammalian hosts."

Laboratory Vector Competence Studies of Some Important Arboviruses from the Americas

Dengue (DEN)

DEN viruses consist of an antigenic subgroup of four closely related, but antigenically distinct, viruses designated DEN-1, -2, -3, and -4, which belong to the genus *Flavivirus*, family Flaviviridae (Westaway et al., 1985).

The classical form of dengue is characterized by an acute febrile illness with headache and joint and muscle pains (WHO, 1986a). Epidemics of dengue annually affect millions of people in tropical areas of the world. Dengue hemorrhagic fever/dengue shock syndrome (DHF/DSS) is a severe form seen primarily in children, although it can affect adults as well. It is caused by the same DEN virus as classical dengue. However, DHF/DSS may have an immunopathologic basis, and the case-fatality rate is 5% to 10% (WHO, 1986a). DHF is a major cause of morbidity and mortality among children in many countries of Southeast Asia, and recently its importance has increased in the Americas (Halstead, 1980; Monath, 1986; Kouri et al., 1989; PAHO, 1992).

In the Americas, dengue worsened as a public health problem during the 1980s. Between 1980 and 1990 more than 1 million dengue cases were reported to PAHO. The majority of these cases were caused by serotypes 1, 2, and 4, with a few imported cases related to DEN-3. During those years, an increase in cases of DHF/DSS was observed in various countries of the continent. Thus far, the most important outbreak of DHF/DSS was in Cuba in 1981, when more than 300,000 dengue cases, 10,312 DHF/DSS cases, and 158 deaths were recorded (Kouri et al., 1989). A second major outbreak occurred in Venezuela from October 1989 to January 1990, with 5,990 cases and 70 deaths (PAHO, 1992). Other countries in the Americas that have reported DHF are Aruba, Brazil, Colombia, the Dominican Republic, El Salvador, French Guiana, Honduras, Mexico, Nicaragua, Puerto Rico, Saint Lucia, Suriname, and the Virgin Islands (Institut Pasteur de Guyane, 1991; PAHO, 1992).

The ability of *Ae. albopictus* to transmit DEN virus was first shown in studies involving human volunteers as early as 1926 (Siler et al., 1926). More recently, *Ae. albopictus* was shown to be able to transmit all four DEN serotypes both horizontally (Gubler and Rosen, 1976) and vertically (Rosen et al., 1983). The species was also found to be more susceptible to oral infection with all four DEN serotypes than was *Ae. aegypti* (Jumali et al., 1979; Rosen et al., 1985). Naturally infected *Ae. albopictus* were collected in Asia by Rudnick and Chan (1965).

Various studies have found *Ae. albopictus* to be associated with epidemics of dengue fever (Chan, Y. C., et al., 1971; Jumali et al., 1979; Fan et al., 1989). However, because *Ae. albopictus* often overlaps in distribution with *Ae. aegypti*, another known vector of DEN viruses, it is often difficult to determine the relative contribution of the two species to disease transmission. During massive dengue epidemics in the Seychelles Islands and in Guandong, China, where *Ae. aegypti* was absent, *Ae. albopictus* was incriminated as the principal vector (Metselaar et al., 1980; Qiu et al., 1981). Thus, experimental and natural association of the four DEN viruses with *Ae. albopictus* has been documented in several instances.

In the Americas, geographical strains of *Ae. albopictus* from Brazil (Cariacica City) and the United States (Houston) are competent laboratory vectors of all four DEN serotypes (Mitchell, 1991). In addition, both North and South American strains of *Ae. albopictus* can transmit all four DEN serotypes vertically (Mitchell and Miller, 1990; Bosio et al., 1992). Thus, *Ae. albopictus* may serve as an important maintenance vector of DEN viruses in endemic areas, and new endemic foci may be initiated by importation of vertically infected eggs (Gubler, 1987; Shroyer, 1990).

Yellow Fever (YF)

YF virus is a member of the genus *Flavivirus*, family Flaviviridae. This viral disease is endemic in tropical regions of both the Americas and Africa. In the Americas, the endemic areas for YF include the Amazon and Orinoco-Magdalena basins in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Peru, and Venezuela (Acha and Szyfres, 1987). The disease may range from subclinical to fatal. Depending on the severity, the signs and symptoms of yellow fever include fever, headache, nausea, epistaxis, albuminuria, and body pain. In severe cases, the disease is characterized by oliguria, jaundice, and hemorrhagic manifestations that include epistaxis, black vomitus, melena, and even uterine hemorrhage (WHO, 1985).

Dinger et al. (1929) reported that *Ae. albopictus* females transmitted YF virus to monkeys in laboratory experiments. However, infection and transmission rates were not determined.

Monath (1986) suggested that, because of the ecological adaptability of *Ae. albopictus*, this species could bridge the gap between the jungle and urban YF viral transmission cycles. This scenario would favor the spread of YF in villages and towns, particularly in endemic areas of South America. *Ae. albopictus* could fill an ecological niche analogous to that of *Ae. simpsoni*, a major bridging and epidemic vector of YF in East Africa. These assumptions have been reinforced by experimental studies indicating that both

the U.S. (Houston) and Brazilian (Cariacica, Espírito Santo State) strains of *Ae. albopictus* are susceptible to oral infection with YF virus (Mitchell et al., 1987; Miller and Ballinger, 1988; Miller et al., 1989). However, the North American strains were significantly more efficient vectors than were their southern counterparts.

Venezuelan Equine Encephalitis (VEE)

VEE virus is a member of the genus *Alphavirus*, family Togaviridae. Based on the kinetics of the hemagglutination-inhibition test, Young and Johnson (1969) first established a classification for VEE virus consisting of a complex group divided into four subtypes (I–IV). Subsequently, six antigenically related virus subtypes numbered I through VI were defined (Walton and Grayson, 1989; Calisher, 1994). Also recognized are the varieties IAB, IC, ID, IE, and IF within subtype I, as well as the varieties IIIA, IIIB, and IIIC, for a total of eight different variants (Calisher, 1994). Among the five antigenic variants of subtype I, two (IAB and IC) are virulent to horses and are responsible for epidemics/epizootics, while the other members of the VEE complex are generally considered enzootic viruses (Calisher, 1994). The VEE complex is native to the Americas and is endemic in Central America and northern South America as well as Mexico, Trinidad and Tobago, and the state of Florida in the United States (WHO, 1985).

VEE in humans is usually a respiratory illness with fever, headache, and muscle pain similar to a self-limiting influenza-like febrile illness. However, some infections develop into a serious encephalitis (Shope, 1985a; Acha and Szyfres, 1987). In most cases, the onset of the disease is accompanied by malaise, chills, cephalalgia, and, frequently, nausea, vomiting, and diarrhea. The illness may resolve after three to five days unless encephalitis occurs. Peripheral neurological symptoms, such as flaccid or spastic paralysis and alterations in reflexes similar to the neurological symptoms of other arbovirus encephalitides, are typical of VEE encephalitis (Acha and Szyfres, 1987). Encephalitis is more frequent in children than in adults. Mortality rates are low but may reach 3.6% in areas with deficient medical services (Shope, 1985a). Sequelae, including behavioral changes and learning defects, also occur. Horses may develop a rapid fulminating illness with sudden death or an encephalitic syndrome. During the period 1967–1971, over 100,000 equine deaths due to VEE, as well as hundreds of thousands of human infections, were reported from Central America and the United States (WHO, 1985).

Experimental studies indicate that both North and South American strains of *Ae. albopictus* are competent vectors of VEE virus (Beaman and Turell, 1991; Turell and Beaman, 1992). However, susceptibility to infection and rates of transmission varied significantly among the five strains tested. Transmission rates were higher for South American strains (24%) than for U.S. strains from Indiana or Texas (5%) (Beaman and Turell, 1991); however, a strain from New Orleans (Gentilly), Louisiana, transmitted VEE virus most efficiently (45%) (Turell and Beaman, 1992). The transmission rate observed for the New Orleans strain is comparable to or even higher than those reported for *Psorophora confinnis* (33%) and *Aedes sollicitans* (38%), two of the natural vectors of epizootic VEE (Sudia et al., 1971b; Turell et al., 1992a). Turell and co-workers (1992a) speculate that the observed differences in strain susceptibility may be the result of either a founder effect or separate introductions in the areas of origin of the strains. The efficient transmission of VEE virus by some of the *Ae. albopictus* strains presently found in the Americas suggests that the presence of this species has increased the risk of transmission of VEE.

La Crosse (LAC)

LAC virus is a member of the genus *Bunyavirus* of the family Bunyaviridae and belongs to the California serogroup. Isolation of LAC virus has been reported only from North America, and LAC is endemic throughout large portions of the midwestern United States. Infection with LAC virus can cause encephalitis, particularly in children and adolescents under 15 years of age. The endemic area includes Minnesota, Wisconsin, Illinois, Indiana, Ohio, West Virginia, and New York. Although fewer than 100 cases are usually reported each year, it is likely that many infections with LAC virus are incorrectly diagnosed as cases of mild, undifferentiated fever of unknown origin. Infection with LAC virus may result in an illness with high fever, with or without generalized convulsions. Vomiting, focal seizures, paralysis, abnormal reflexes, and mental manifestations are common (Shope, 1985b), and neurological sequelae can persist for years after the acute illness. The case-fatality rate is less than 0.5%.

Various species of mammals, especially rodents, are susceptible to infections by LAC virus, but it is believed that these infections are generally asymptomatic (Acha and Szyfres, 1987). The tree hole mosquito *Aedes triseriatus* is considered to be the principal vector of LAC virus to both amplifying rodent hosts and humans. The main vertebrate hosts of LAC appear to be the eastern chipmunk (*Tamias striatus*), gray squirrel (*Sciurus carolinensis*), and red fox (*Vulpes fulva*) (Calisher, 1994).

The introduction of *Ae. albopictus* into areas enzootic for LAC has led to various studies of the vector potential of this species for LAC virus (Tesh and Gubler, 1975; Grimstad et al., 1989; Streit and Grimstad, 1990; Cully et al., 1991; Cully et al., 1992). *Ae. albopictus* is highly susceptible to oral infection with LAC virus, as nearly all (1,633 or >99%) of 1,637 *Ae. albopictus* contained LAC virus when tested 14 days after ingestion of a blood-LAC virus

suspension containing virus titers simulating doses that would be encountered in nature (3.5–4.5 logs). These studies included 27 strains of *Ae. albopictus*, 14 from locations within the continental United States, 5 from Brazil, and the rest from temperate Asia, tropical Asia, and Hawaii (Streit and Grimstad, 1990). Moreover, 97% of the 1,637 were head-positive for the virus, suggesting dissemination of LAC virus beyond midgut barriers and throughout the hemocoel. All 43 *Ae. triseriatus* fed on the same blood-virus suspension also had disseminated LAC virus infections (Streit and Grimstad, 1990). Other experiments conducted with LAC-viremic eastern chipmunks (*T. striatus*) suggest that the infection threshold of *Ae. albopictus* is lower than that of *Ae. triseriatus* (Streit, pers. comm., 1993). More than 30% of fully engorged *Ae. albopictus* became infected, compared to less than 10% of similarly exposed *Ae. triseriatus*, after feeding on a chipmunk with a LAC virus titer of 3,600 viral plaque-forming units (PFU)/ml blood (84 hour postinfection). In transmission experiments conducted after 14 days of extrinsic incubation, 43% of *Ae. albopictus* transmitted virus to suckling mice (Streit and Grimstad, 1990). *Ae. albopictus* infected either orally or transovarially transmitted LAC virus to susceptible eastern chipmunks (Cully et al., 1992). As with other arboviruses, there was significant variation in transmission rates (18%–75%) among the various *Ae. albopictus* strains tested. Brazilian and tropical Asian strains tended to transmit LAC virus more efficiently than did North American and temperate Asian strains (Streit and Grimstad, 1990).

Ae. albopictus also can transmit LAC virus transovarially (Streit and Grimstad, 1990; Cully et al., 1992). Minimum filial infection rates range between 1% (Teresa Brazilian strain) and 4.5% (Oahu strain). In a recent study, filial infection rates ranged from 3%–22% (average 10%) for progeny of individual LAC virus-infected females (Streit and Grimstad, 1990). Streit (1994) found that transovarial transmission of LAC increased rapidly with selection. After three generations, he established a LAC-disseminated line which continued 90%+ positive for 10 generations. In another line he established, transovarial transmission continued for 10 generations among mosquitoes that never received blood (i.e., were completely autogenous). This ability opens remarkable possibilities for the maintenance of a reservoir. In an economically depressed area in East St. Louis, Illinois, 50% of wild-caught *Ae. albopictus* had fed on urban rats. Antibodies to LAC were found in rats and opossums. Streit (1994) suggests the possibility of a new urban cycle for LAC.

The fact that *Ae. albopictus* becomes infected and transmits LAC virus at rates similar to those of the natural vector (*Ae. triseriatus*), along with its establishment in areas where LAC virus is endemic and its general feeding behavior, indicates that *Ae. albopictus* may become involved in the natural LAC virus cycle and serve as a secondary vector in areas where LAC virus is active.

Mayaro (MAY) and Oropouche (ORO)

MAY virus is a member of the genus *Alphavirus*, family Togaviridae. Its activity has been documented only in the Americas, where it has been isolated in Bolivia, Brazil, Panama, Suriname, Trinidad, and the United States (Pinheiro and LeDuc, 1989). In endemic areas, such as the Amazon regions of Bolivia and Brazil, 10%–15% of residents have antibodies to MAY virus (Pinheiro and LeDuc, 1989). The onset of the illness is abrupt, with fever, headache, epigastric pain, backache, arthralgia, photophobia, dizziness, and chills (Pinheiro et al., 1981; Pinheiro and LeDuc, 1989). Humans appear to be accidental hosts that become infected in forest areas where MAY virus circulates among wild vertebrates and mosquitoes. MAY virus has been isolated from several species of mosquitoes, especially *Haemagogus* spp., although it has also been recovered from *Culex*, *Sabethes*, and *Aedes* spp.

A strain of *Ae. albopictus* from São Paulo, Brazil, was a competent laboratory vector for MAY virus, with infection rates of 9%–85% and transmission rates of 45%–50% (Smith and Francy, 1991).

It was concluded that "with large *Ae. albopictus* populations and extensive MAY virus amplification, this species could serve as a secondary vector during outbreaks and perhaps as a bridging vector for MAY virus between the forest habitats and settled areas" (Smith and Francy, 1991). The danger that *Ae. albopictus* will become involved in the transmission cycle of this virus is increased by the recently reported infestations of *Ae. albopictus* in the state of Maranhão, which is contiguous with the state of Pará, where past outbreaks of MAY have been reported (Pinheiro et al., 1981).

ORO is a member of the Simbu serogroup of the genus *Bunyavirus*, family Bunyaviridae (Karabatsos, 1985). Infection with ORO virus has been recognized as a major cause of human febrile illness in the Amazonian region of Brazil. Between the years 1962 and 1980, several outbreaks occurred in Pará State which affected at least 165,000 persons in various urban centers (Pinheiro et al., 1982). Although no deaths have been attributed to infection with ORO virus, many patients became severely ill and required a prolonged convalescence (Shope, 1985b). The disease is manifested by a sudden onset of fever, chills, and malaise and is marked by myalgia, dizziness, headache, photophobia, and sometimes mild epigastric pain, nausea, and vomiting.

Studies carried out with an *Ae. albopictus* strain from São Paulo, Brazil, suggest that this species may not be a competent vector of ORO virus (Smith and Francy, 1991). Infection rates were 2%–12%, and no mosquito of this strain transmitted the virus by bite. This is not surprising, since *Culicoides paraensis* is considered the natural vector (Pinheiro et al., 1982). However, although the risk that *Ae. albopictus* will become involved in ORO virus transmission

appears low based on the results of Smith and Francy (1991), other strains of *Ae. albopictus* might be more efficient vectors of the virus.

Arboviruses Common in Areas Outside the Americas

Ae. albopictus is a competent vector of several viruses not endemic to the Americas. These include Japanese encephalitis (JE), chikungunya (CHIK), Ross River (RR), Sindbis (SIN), and West Nile (WN) viruses. In addition, *Ae. albopictus* can transmit JE virus transovarially, raising the possibility that JE virus could be introduced into the Americas via infected eggs. Information on JE, SIN, CHIK, and RR viruses is summarized below.

Japanese Encephalitis (JE)

JE virus is a member of the West Nile antigenic complex of the genus *Flavivirus*, family Flaviviridae. Monath (1985) considers the disease it causes to be the most important of the arboviral encephalitides in terms of morbidity and mortality. Epidemics of JE recur seasonally in temperate areas of Asia and in the northern part of tropical Southeast Asia. Illness may be manifested as a febrile headache syndrome, aseptic meningitis, or encephalitis. When neurological disorders appear, they are usually accompanied by fever, chills, anorexia, nausea, vomiting, dizziness, and drowsiness. Case-fatality rates during epidemics range from 20% to 50%, but these high rates reflect recognition of only the most severe cases.

In the laboratory, *Ae. albopictus* is susceptible to infection with JE virus and is able to transmit virus vertically to its F_1 progeny after either intrathoracic inoculation or ingestion of a virus-sucrose-erythrocyte mixture (Rosen et al., 1978). As adults, at least five of the infected F_1 female *Ae. albopictus* transmitted JE virus to chicks on which they fed. Moreover, Huang (1982) reported that seven strains of the JE virus were isolated from field-collected *Ae. albopictus* larvae from Fukien, China.

Sindbis (SIN)

SIN virus is a member of the western equine encephalitis complex of the genus *Alphavirus*, family Togaviridae, and causes a dengue-like disease in humans. Clinical symptoms include fever, rash, headache, general malaise, and arthralgia (Niklasson, 1989). Although no fatal cases have been reported, arthralgia may be severe enough to require hospitalization and may persist for up to three years. SIN occurs in Europe, Africa, Asia, and Australia. Various *Culex* spp. have been implicated as potential vectors, and the natural transmission cycle is believed to be between *Culex* mosquitoes and birds, with various *Aedes* spp. acting as bridge vectors that infect humans.

Laboratory studies indicate that *Ae. albopictus* is at least as efficient a vector of SIN virus as is *Cx. pipiens*, a known vector (D. Dohm and M. Turell, unpublished data). SIN virus has not yet been recovered from wild specimens of *Ae. albopictus*.

Chikungunya (CHIK)

CHIK virus is also a member of the genus *Alphavirus*, family Togaviridae, and causes a dengue-like disease in humans. This disease has an abrupt onset, with high fever, myalgia, and sudden intense pain in one or more joints (Shope, 1985a). Outbreaks of chikungunya fever have been recognized in Angola, Congo, Nigeria, Senegal, and Zimbabwe in Africa and in Cambodia, India, Malaysia, the Philippines, and Thailand in Asia (Karabatsos, 1985); these outbreaks affected tens of thousands of people.

Ae. albopictus adults are highly susceptible to infection with CHIK virus in laboratory experiments and also are capable of transmitting the virus by bite (Mangiafico, 1971; Yamanishi et al., 1983; Turell et al., 1992a). High infection and transmission rates for *Ae. albopictus* (100% and 69%, respectively) readily testify to the importance of this mosquito as a potential vector of CHIK virus (Mangiafico, 1971). Furthermore, Turell and colleagues (1992b) demonstrated high infection rates (range, 72%–97%) in eight *Ae. albopictus* strains from different areas of Asia, Brazil, and the United States after the mosquitoes fed on a viremic rhesus monkey. Dissemination rates (36%–80%) observed in the experiments were higher than those found in *Ae. aegypti*, the natural vector of CHIK virus in Southeast Asia. Transmission rates were not calculated. The virus has not yet been recovered from wild specimens of *Ae. albopictus*.

Ross River (RR)

RR virus is a member of the genus *Alphavirus* and the etiologic agent of epidemic polyarthritis (EPA) (Shope, 1985a; Mitchell and Gubler, 1987). Individuals affected by the disease complain of pain, swelling, and limitation of movement in the joints of the hands and ankles. Patients may develop a maculopapular rash on the trunk and extremities. Other symptoms include sore throat, enlarged lymph nodes, and tender palms and soles (Shope, 1985a). Until the late 1970s, reports of epidemics of EPA were initially received only from Australia, the Solomon Islands, and New Guinea. In 1979 a major outbreak of EPA occurred in the Western Pacific region, affecting more than 50,000 individuals in Fiji, the Samoan Islands, the Cook Islands, and parts of Melanesia (see references in Mitchell and Gubler, 1987). Antibodies for the virus have been found in domestic animals such as dogs, sheep, pigs,

horses, and cattle. Antibodies also have been found in wild mammals such as kangaroos, wallabies, and rodents (Shope, 1985a). The most important vectors of RR virus appear to be *Culex annulirostris*, *Aedes vigilax*, and *Aedes polynesiensis* (Kay et al., 1982).

Studies on the vector competence of several geographical strains of *Ae. albopictus* from Houston, Hawaii, and Asia showed the species to be an efficient experimental vector for RR virus (Mitchell and Gubler, 1987; Mitchell et al., 1987). Variation in vector competence among the geographical strains was also detected in the trials. Infection rates approached 100% following ingestion of high-titer blood meals from golden Syrian hamsters (6.3 $\log_{10}$ PFU/ml–7.1 $\log_{10}$ PFU/ml). Strains from Sri Lanka and Singapore demonstrated less susceptibility to infection (53%–80%). Transmission rates were also high in the Houston and Hawaii strains (52% and 77%, respectively) by day 14. Both strains were able to transmit RR virus to suckling mice by day 7 postinfection. When larvae from the second oviposition of an infected female parent were tested, they failed to show proof of vertical transmission. Ross River virus has not yet been recovered from field-collected *Ae. albopictus*.

Transovarial Transmission

In addition to a high susceptibility to oral infection, *Ae. albopictus* is able to transmit numerous viruses to its progeny transovarially. Strains of *Ae. albopictus* from Hawaii or Asia are known to be able to transmit vertically 15 arboviruses: DEN-1, DEN-2, DEN-3, DEN-4, Banzi, Bussuquara, Ilheus, Kokobera, Kunjin, JE, SLE, and Uganda S viruses in the family Flaviviridae; and KEY, LAC, and San Angelo viruses in the family Bunyaviridae (Tesh, 1980; Shroyer, 1986). Stabilized infections of San Angelo virus occur in *Ae. albopictus*, and very efficient vertical transmission takes place for up to 38 consecutive generations (Tesh and Shroyer, 1980; Shroyer, 1986). In the laboratory, *Ae. albopictus* strains from the Americas have vertically transmitted DEN-1, DEN-4, YF, POT, and LAC viruses (Mitchell, 1991; Streit and Grimstad, 1990).

Other Arboviral Studies

Shroyer (1986) lists some arboviruses that are able to replicate in *Ae. albopictus* specimens following intrathoracic inoculation. However, there is no information on whether *Ae. albopictus* can be orally infected with these arboviruses and subsequently transmit them by bite. These viruses include the phleboviruses Arumowat, Bujaru, Chilibre, Icoaraci, Itaporanga, Karimabad (Tesh, 1975), and Rift Valley virus (Turell et al., 1988), and the rhabdoviruses Chandipura, Gray Lodge, Joinjakaka, Piry, Sigma, and vesicular stomatitis (Rosen, 1980).

Protozoan and Filarial Diseases

Filarial Worms

Field-collected specimens of *Ae. albopictus* from Sanglaburi, Thailand, were found to be infected with *Dirofilaria* spp. (Harinasuta et al., 1970). *Ae. albopictus* is considered an important vector of *Dirofilaria immitis*, the causative agent of dog heartworm in Japan and the United States (Mori and Wada, 1977; Scoles and Craig, 1993). *Ae. albopictus* populations from the United States have marked genetic variability in terms of susceptibility to *Dirofilaria immitis*. Work carried out in North Carolina found that *Ae. albopictus* was entirely refractory to infection with *D. immitis* (Apperson et al., 1989). However, more recent work conducted at the University of Notre Dame showed that 40% of an *Ae. albopictus* population from New Orleans developed infectious L3 larvae; the results for other U.S. populations were intermediate (Scoles and Craig, 1993). Several laboratory experiments also have demonstrated that *Ae. albopictus* can be infected with *D. immitis* (Galliard and Ngu, 1938; Stojanovich and Scott, 1965; Konishi, 1989).

However, *Ae. albopictus* is not a vector of human filariasis caused by *Brugia* or *Wuchereria* spp. (Sasa, 1976). The larval worms fail to develop in the thoracic muscles. Rosen et al. (1976) justified their release of *Ae. albopictus* on a small Pacific atoll as an attempt to replace a vector of filariasis (*Ae. polynesiensis*) with a nonvector. Unfortunately, *Ae. albopictus* failed to persist on the atoll.

Avian Malarias

Avian malarias have been experimentally transmitted by *Ae. albopictus*. The species became infected with and transmitted *Plasmodium lophurae* beginning 12 days after feeding on an infected duck (Laird, 1941). Likewise, *Ae. albopictus* is susceptible to infection with *Plasmodium gallinaceum*; female mosquitoes developed sporozoites in the salivary glands and gut 15 days after an infectious blood meal (Russell and Menon, 1942). These mosquitoes also transmitted *P. gallinaceum* to normal fowls. The ability of *Ae. albopictus* to harbor *P. gallinaceum* has made this mosquito a useful model for malaria studies (Hu et al., 1989).

DISSEMINATION AND CONTROL

Mode of Dissemination and Origin

Since the discovery of *Ae. albopictus* in the Americas in 1985 and its rapid spread to more than 300 counties in 23 states of the continental United States and 673 municipalities in 7 states in Brazil (C. Moore, pers. comm., September 1994; J. Mangabeira da Silva, pers. comm., April 1994),

questions have arisen as to how the mosquito was introduced in the first place and how it is spread to new areas.

The spread of *Ae. albopictus* is widely believed to be associated with the massive movement of used tires around the world (Rai, 1991). There is compelling evidence that used tires imported in containers from Asia and holding larvae and ova of *Ae. albopictus* are responsible for its introduction into the United States (Monath, 1986; Craven et al., 1988; Francy et al., 1990b). After the Houston experience, in which tires were found to be the main breeding source of *Ae. albopictus* (Sprenger and Wuithiranyagool, 1986), surveys carried out in other states have focused on tire yards.

The recent infestations of *Ae. albopictus* reported in towns along the northern border of Mexico in the states of Coahuila and Tamaulipas may also be due in part to the movement of used tires and other artificial containers. It is important to note that the officially reported figures on the number of used tires exported from the United States to Mexico have been increasing steadily since the 1980s. Furthermore, Mexico is the principal customer for U.S. used tires in the Western Hemisphere, having bought 173,708 units in 1991 alone (U.S. Department of Commerce, Bureau of the Census, National Trade Data Bank, CN TRADEX A4012200000—Used pneumatic tires of rubber). In addition, it is well known that many trucks transport scrap tires from infested areas of the United States throughout Mexico, which clearly favors the spread of the infestation. Thus, it is uncertain whether the Mexican infestations are restricted to those areas bordering the state of Texas or whether the species has already become well established in the country.

In the four countries in the Americas known to harbor the species—Brazil, the Dominican Republic, Mexico, and the United States—*Ae. albopictus* has been reported breeding in tires, as well as in artificial and natural water-filled containers. Regarding the issue of used tire exports, O'Meara and co-workers (1993) pointed out that "there is a major threat of exporting *Ae. albopictus* from the United States to countries that are currently free of this mosquito. Used tires are being shipped from Florida and other Gulf Coast states, without adequate inspections for mosquitoes, to destinations in the Caribbean region and Central and South America." Introduction of *Ae. albopictus* to additional countries in the Americas would appear to be imminent or may have already occurred owing to such factors as the rapid expansion of commerce and traffic by land, air, and sea. Moreover, since adequate entomological surveillance and vector control activities are lacking in most of the countries of the Americas, the spread is likely to continue.

In the state of Florida, three other specific factors besides the movement of containers appear to be contributing to the spread of the species. These factors are the widespread availability of suitable aquatic habitats, the decline of *Ae. aegypti* populations, and the rapid adaptation of *Ae. albopictus* to shorter photoperiods (O'Meara et al., 1993). Moreover, since 1986, in many areas in Louisiana *Ae. albopictus* has shown that it can spread from tire piles into tree holes (NOMCB, 1987).

The appearance of the species in the Dominican Republic raises several unanswered questions. The infestation may be a strain of temperate origin (from either Asia or continental America) that originally had a photoperiodic response but progressively lost it as a result of genetic selection for a nonphotoperiodic trait. Another possible scenario is that this infestation is independent of others in the Americas, having been brought inadvertently in shipping cargos that originated in tropical Asia. Current research will undoubtedly answer these questions in the near future.

Brazil's infestation appears to be linked to the international seaport of Victoria in the state of Espírito Santo (PAHO, 1987). Since used tires from the United States are regularly unloaded in this area, it is possible that a secondary dispersion of *Ae. albopictus* may have been responsible for its introduction into Brazil. It thus appears that all the infestations reported from the Americas are classic examples of the role played by increased travel and commerce between countries in the proliferation of a non-native species.

Studies on North American and Brazilian strains of *Ae. albopictus* have shown that populations from both areas are electrophoretically similar to *Ae. albopictus* populations from temperate areas of northern Asia (Kambhampati et al., 1991).

In the United States, studies carried out to determine the degree of differentiation among mosquitoes collected at several sites in the same city and among populations from different cities showed levels of genetic variation in the Houston and New Orleans populations. These results suggested large and independent introductions of *Aedes* to both cities and support the idea that Houston and New Orleans (Black et al., 1987) were the first sites of introduction in the United States.

Overall, enzyme electrophoretic observations carried out by Drs. W. Hawley and L. Munstermann with Southeast Asian populations of *Ae. albopictus* show extreme genetic differentiation, in marked contrast to the relative homogeneity of North American populations. "This appears to indicate that gene flow in the introduced populations of the Americas is much higher than that found among indigenous populations" (Hawley, pers. comm., 1991). Other molecular studies appear to reinforce the notion of high levels of gene flow in the species. For instance, variation in mtDNA was analyzed in 17 populations of *Ae. albopictus* using 18, 4, 5, and 6 bp cutting restriction enzymes (Kambhampati and Rai, 1991). The results revealed a low level of restriction fragment length polymorphism in the *Ae. albopictus* populations, compared with other insect species. Only three populations were found to carry novel mtDNA haplotypes. An analysis of individual mosquitoes revealed that these populations included individuals carrying both the ancestral

and the novel mtDNA haplotypes, suggesting that the divergence of the populations is incomplete. The study concluded that the recent range expansion of the species and gene flow facilitated by human activities could explain the low level of polymorphism. Rai (1986 and 1991) reviewed studies on the genetics of *Ae. albopictus*.

In general, it is believed that populations that are highly variable, i.e., genetically plastic, are better able to avoid control measures and to develop resistance. Partial resistance to organophosphates, specifically malathion, has arisen in *Ae. albopictus* populations from Houston and New Orleans (NOMCB, 1987; Khoo et al., 1988; Robert and Olson, 1989). Various levels of resistance to organophosphates have been observed in several populations in the United States, while Brazilian strains from Espírito Santo State (Cariacica City) have been found to be highly susceptible to the insecticides studied (Wesson, 1990).

Control

It is more difficult to control or eradicate *Ae. albopictus* than *Ae. aegypti* because *Ae. albopictus* is found farther from human habitation and in a wider range of habitats. Population suppression may be economical only in areas near human communities. Clearly, the best approach for controlling *Ae. albopictus* and other *Stegomyia* species is to limit the availability of larval habitats. Massive educational programs encouraging citizens to take actions to prevent mosquito breeding around and in their homes can play a central role in control efforts.

Prior to the U.S. infestation, very few studies or evaluations dealt with the control of *Ae. albopictus*. In fact, this species was rarely, if ever, the primary target of a control program. More often, it was considered secondary in importance to *Ae. aegypti*. To date, the most extensive effort to control *Ae. aegypti* and *Ae. albopictus* has been carried out in Singapore. This integrated program, begun in 1968, includes environmental management, health education, legal measures, and community participation; chemical control is reserved solely for outbreaks of dengue hemorrhagic fever (WHO, 1986b).

Chemical Control

House-to-house control campaigns, directed specifically at *Ae. aegypti*, appear to be less effective against *Ae. albopictus*, whose control requires coverage of larger areas, including the forest. For instance, on an island in the Gulf of Thailand, temephos applications and malathion fogging effectively suppressed the *Ae. aegypti* population but did not significantly reduce the *Ae. albopictus* population (Gould et al., 1970).

Dowling (1955) reported control of *Ae. albopictus* using 15% dieldrin applied at 88 ml per ha with a SwingFog® portable thermal fog generator. With one treatment of an entire 11.5-km^2 island near Singapore, good control was achieved for 10 days; however, the population recovered rapidly during the third week. With two treatments spaced a week apart, more prolonged control was achieved (a 92% reduction for up to eight weeks).

As already stated, in Singapore, chemical control is used only during outbreaks of dengue hemorrhagic fever. During one such epidemic in 1973, special attention was given to 400 construction sites where vector breeding places and harborages were profuse. To kill the adult mosquitoes, all the construction sites were fogged with bioresmethrin mixed with equal parts of piperonyl butoxide as a synergist; the containers were treated with 1% temephos sand granules or 1% malathion emulsion to kill the immature stages. The DHF cases continued, however, so continuous daily treatment was implemented at these sites. This approach resulted in a significant drop in DHF incidence (WHO, 1986b).

In Louisiana, ultra-low-volume (ULV) application of the synthetic pyrethroid bioresmethrin reduced the adult *Ae. albopictus* population by 60%, but the reduction lasted for only about three days (Anderson, New Orleans Mosquito Control District, pers. comm., 1986). In New Orleans, formulations of permethrin sandcore granules containing 1.5% active ingredient were tested to control larvae in experimental plots containing tire piles. The pesticide was applied using manually operated sprayers. The approximate mean weight per treated tire was 8 g. A single application produced larval control of nearly 100% during a period of 121 days (NOMCB, 1987) and greater than 80% for nearly 300 days (NOMCB, 1988). A similar experiment, also carried out in tire piles in New Orleans, was conducted to assess the effects of a combination of corncob fenoxicarb-impregnated material (1% active ingredient) and granular formulations of Bti (*Bacillus thuringiensis* var. *israelensis*) (200 ITUs). The mean weight of granules received in each tire was 5.8 g. Mortality of larvae in the treated tires exceeded 80% at 60 days, but fell to 9% at 81 days (NOMCB, 1987).

During the summer of 1989 aerial ULV malathion treatments were conducted in two urban areas of New Orleans. The twin-engine aircraft were equipped with two self-contained Micronair spray pod systems utilizing rotary atomizers. Aerial treatment rates were 3 oz/acre, at a treatment altitude of 120–200 feet and flight speed of 150 mph, resulting in a swath width of 500 feet; this treatment succeeded in suppressing the population of *Stegomyia* mosquitoes for seven or more days (NOMCB, 1989).

Jardina (1990) reported the eradication of *Ae. albopictus* from Indianapolis in Marion County, Indiana, through a combination of chemical treatment and source reduction (removal of tires and trash from yards). The classical treatment of malathion and granular Abate was replaced with synergized resmethrin and granular Bti. In September 1987,

adulticiding was performed around an infested tire retreading company and surrounding roads using a ULV fogging unit mounted on a truck. Synergized resmethrin was used at a rate of 130 ml/min during five consecutive days. The operation was conducted twice a day at the optimal spraying times of mid-morning and early evening. In addition, a portable ULV unit was used in inaccessible areas. Simultaneously, larvicide operations with Bti were carried out in 3,500 tires six times during a period of 45 days. Surveillance operations conducted in 1988 and 1989 failed to detect any *Ae. albopictus* in the area.

Other studies of *Ae. albopictus* populations from around Houston, Texas, demonstrated the adulticidal effects of resmethrin, which produced 96% mortality at concentrations of 1.5 ng/female (48 hours posttreatment at 21 °C) (Khoo et al., 1988). Another pyrethroid showing moderately toxic effects on *Ae. albopictus* strains from Malaysia is cyfluthrin (Responsar) (Vythilingam et al., 1992). Both wettable and emulsifiable concentrates of cyfluthrin sprayed on plywood (10 mg [ai]/m^2) produced about 60% mortality after 20 days of exposure.

Studies carried out with U.S. strains of *Ae. albopictus* have shown considerable variation in the response of various geographical populations to organophosphate insecticides (Khoo et al., 1988; Robert and Olson, 1989; Wesson, 1990; Sweeney, 1993). According to Wesson (1990), there are two possible reasons for the variation in insecticide susceptibility among the U.S. strains: the U.S. populations may have originated from a number of different Asian areas with distinct insecticide exposure conditions, or selection for insecticide resistance may have taken place in the United States since *Ae. albopictus* became established. Wesson theorizes that the observed differences may be the result of both factors. Some selection for insecticide tolerance to malathion is believed to have taken place in populations from Texas and Louisiana.

Brown (1986) and Neng et al. (1993) report that *Ae. albopictus* is resistant to the organochlorines DDT and HCH in China, India, Japan, Malaysia, Southeast Asia, and the Philippines and resistant to the organophosphate malathion in Singapore and Viet Nam, fenthion in Malaysia, and fenitrothion in Madagascar.

Biological Control

With the exception of the trials carried out with cyclopoid copepods (Marten, 1990a, 1990b), there have been few field trials of predators, parasites, or pathogens of *Ae. albopictus*. Reports have been limited mostly to findings of field infections and species associations.

The predatory mosquito larva *Toxorhynchites splendens* was found to be frequently associated with *Ae. albopictus* in Singapore, and Chan (1968a) concluded that "... *T. splendens* can probably be most effectively utilized for the control of *Aedes albopictus* in rural areas. . . ." On the other hand, Newkirk (1947) believed that *T. splendens* would occupy a minor role in the elimination of mosquitoes: "Its long life and few offspring, when compared to *Aedes albopictus*. . . , and its low survival rate tend to nullify the importance of (*T.*) *splendens* in biological control." An attempt to reduce the breeding of *Ae. albopictus* by introducing small numbers of *T. inornatus* in Hawaii in the 1920s failed when this predator died out (Gerberg, 1985).

The technology developed for the mass rearing and field trials of *T. brevipalpis* and *T. rutilus* for the control of *Ae. aegypti* in the Americas (Gerberg, 1985) may be utilized with even better results against *Ae. albopictus*, since both the latter species and these predators breed readily in natural containers away from homes, while the breeding sites of *Ae. aegypti* are more domestic.

In laboratory tests with the parasitic mermithid nematode *Romanomermis culicivorax*, *Ae. albopictus* was rated "3" on a susceptibility scale of 1 to 5, indicating that the host showed moderate physiological resistance (Finney-Crawley, 1985).

Roberts et al. (1983) report two observations of laboratory infection of *Ae. albopictus* with viruses: densonucleosis virus, which only retarded growth at low temperatures (16 °C), and *Nodamura* virus, a small RNA virus that infects vertebrates. This virus caused death in *Ae. albopictus* when inoculated into the thorax but little mortality when ingested by adults or immersed larvae.

In the laboratory, susceptibility of *Ae. albopictus* to the bacterium *Bacillus thuringiensis* var. *israelensis* was found to be lower than that of *Ae. aegypti* from Enugu, Nigeria, and Djakarta, Indonesia, but higher than that of *Ae. aegypti* from Bora Bora (de Barjac and Coz, 1979).

Infection with three species of gregarine protozoans of the genus *Ascogregarina* was observed in *Ae. albopictus* in Taiwan (Lien and Levine, 1980). Beier and Craig (1985) state, "Although many workers have suggested the potential of gregarines as control agents, these parasites appear to be relatively harmless to their natural mosquito hosts."

Various species of the pathogenic fungus *Coelomomyces* were found parasitizing *Ae. albopictus* larvae from bamboo stumps and tree holes in Taiwan between 1955 and 1967 (Laird, 1967). Two species of this fungus (predominantly *C. stegomyiae*) that parasitized *Ae. albopictus* in Singapore were collected and introduced into three atolls of the Tokelau Islands, New Zealand, in 1958. After two years the fungi had significantly reduced the population of *Ae. polynesiensis*, and by 1963 there was a fourfold increase in parasitized larvae (Laird, 1967).

Finally, the use of copepods (*Mesocyclops*), discussed earlier as larval predators, has been demonstrated in field trials in New Orleans (Marten et al., 1989a; Marten, 1990a, 1990b). Several species of cyclopoid copepods that occur naturally in New Orleans, such as *Macrocyclops albidus*, *Mesocyclops longisetus*, and *Mesocyclops aspericornis*,

have been shown to be highly effective for controlling first instar larvae of *Ae. albopictus* in discarded tires. The most effective of the three appears to be *Macrocyclops albidus,* which, at a density of 72 per tire, killed an average of 45 larvae in a 24-hour period. Treatment of tires with this copepod has provided control for a period of two years (Marten, 1990b). Survival of this species is excellent when it is introduced into tires around wooded areas.

Another species that has shown promise in controlling *Ae. albopictus* first instar larvae is *Mesocyclops longisetus.* This species appears to be highly effective in tires situated in the open and exposed to hot summer conditions. Nineteen specimens can eliminate 40 larvae per day. The disadvantage of *Mesocyclops longisetus* is that the species does not survive the winter season, and it is more sensitive to freezing temperatures than *Macrocyclops* (Marten, 1990b).

Another approach that has been recently introduced involves treating tire piles with mixtures of copepods and Bti. Such treatment has been found to provide control for about one year. Bti at concentrations of 1,200 ITU/ml mixed with *Macrocyclops albidus* had no detectable toxic effect on the cyclopoid, but killed both late instars and new instars effectively (Marten et al., 1993).

Environmental Control

Environmental management involves the elimination or reduction of vector breeding sources. Commonly known as source reduction, it appears to be the single most effective method of *Aedes* vector control thus far available. The underlying principle of source reduction consists of the elimination of breeding sources in order to disrupt the immature life cycle of the mosquito. This objective can be implemented by such simple measures as burying or destroying unwanted water-bearing receptacles. Particular attention should be given to reducing standing water in and around seaports, bus terminals, train stations, and airports, as well as in containers such as discarded tires, which are favorite breeding sites of the *Aedes* species. Additional actions that can be taken include upending large containers such as jars, drums, and water tanks that are kept in the open and covering water-holding containers with tight-fitting lids. People can be encouraged to change the water weekly in containers around their homes, such as water jars, flower vases, and ornamental jars, and to scrub and thoroughly rinse these containers to dislodge *Aedes* eggs before refilling with water. Achieving permanent mosquito control in natural containers such as tank bromeliads is difficult, but homeowners may consider limiting the numbers of these plants that they place in their yards. In areas such as Florida it is recommended that tank bromeliads be flushed out twice a week with a garden hose equipped with an appropriate nozzle (O'Meara and Gettman, 1991).

In Singapore, where *Ae. albopictus* populations were found to have three peaks during the year, fluctuating in step with rainfall, the best control measures were aimed at preventing the population peaks by destroying the major breeding sources during the period immediately prior to those peaks (WHO, 1986b).

The most effective form of environmental control is to modify completely and permanently the area where mosquito production occurs. Slums, which were the areas responsible for most *Aedes* breeding in Singapore, have been virtually eliminated by a government housing program. By 1984, more than 75% of the total population was housed in government-constructed apartment buildings. However, this effort did not solve the problem of infestations in large houses with compounds, because although *Ae. aegypti* indices in such houses were low, *Ae. albopictus* house infestation was almost 100%. This was the case because these premises usually had suitable *Ae. albopictus* breeding habitats, such as tin cans, tree holes, and leaf axils of plants (WHO, 1986b).

Health Education

Public health education is aimed particularly at the neighborhoods where *Aedes* indices are highest. To motivate people to eliminate and prevent mosquito-borne diseases, a number of public awareness campaigns can be implemented. These may involve the holding of seminars, workshops, and exhibitions; the distribution of pamphlets and posters; the preparation of feature articles for newspapers and magazines; the presentation of talk shows and the use of slogans on the radio, on television, and in schools; the use of film strips; and the personal message of the vector control officer working door-to-door. In Singapore, it was concluded that "there is no doubt that continuous routine health education measures contributed immensely to the prevention and control of *Aedes* breeding in premises" (WHO, 1986b).

Legal Measures

The legal component of *Aedes* control has two aspects: laws that permit the health inspector to enter each building and examine all potential breeding sources, and legislation that makes it illegal to have breeding places on the premises. In Singapore, the Destruction of Disease-Bearing Insects Act permits the control officer to serve orders and summonses on offenders who maintain conditions conducive to breeding or harboring mosquitoes. For a private homeowner, an order is served when breeding has been confirmed.

To lessen the likelihood that *Ae. albopictus* will move from the United States to other countries of the Americas, the Centers for Disease Control and Prevention has pro-

posed a discussion of the following four options: (a) develop and implement regulations to require disinsection of all used tires exported from the United States; (b) formulate guidelines for use by PAHO countries to require fumigation of used tires shipped from the United States; (c) maintain constant surveillance in port areas and at destinations of imported used tires in each receiving country; and (d) provide assistance by CDC through PAHO to countries wishing to design surveillance and control plans (CDC, 1993).

Integrated Control

No single control method is ever sufficient to lower mosquito levels for a long period of time. Instead, it is necessary to combine the various methods of the vector control arsenal in the most effective, most economical, and safest possible way. In Singapore, a system of routine vector surveillance, continuous year-round source reduction, health education, and fogging of premises in areas where more than 5% of the houses are infested was implemented in 1974. This system was effective in achieving year-round control of the vectors *Ae. aegypti* and *Ae. albopictus*, and was also successful in preventing two epidemics that swept through other parts of the region (WHO, 1986b).

CONCLUSIONS

Some health officials and members of the scientific community have suggested that *Ae. albopictus* is a less important vector of dengue virus than *Ae. aegypti*. Experience in Asia over the past 30 years supports this contention in that, with only a few exceptions, the major epidemics of dengue and dengue hemorrhagic fever have been transmitted by *Ae. aegypti*. Nevertheless, the threat of *Ae. albopictus* in the Americas should not be underestimated. Craig (1993) points out the differences that exist between the two *Stegomyia* species in the Americas and describes them as follows:

- *Ae. albopictus* has a far greater geographical range than *Ae. aegypti* because of its cold tolerance.
- *Ae. albopictus* has a more inaccessible habitat because it breeds in plants, and therefore it is far harder to control.
- The species have different habitats, with *Ae. aegypti* found in the inner city and *Ae. albopictus* in suburban and rural areas.
- *Ae. albopictus* has already achieved far greater populations in the United States than *Ae. aegypti*, which has never been a major biting pest in that country; for example, in New Orleans, 80% of the mosquito complaints are currently about *Ae. albopictus*.
- *Ae. albopictus* can harbor the same range of arboviruses and is a more efficient vector for some of them; *Ae. aegypti* has never been known to enter into the cycle of EEE.
- *Ae. albopictus* has the potential to enter into the La Crosse virus cycle, while *Ae. aegypti* has no chance of doing so because it cannot survive the winter cold.
- *Ae. albopictus* can feed on a wide variety of hosts, while *Ae. aegypti* outside Africa is highly domestic and is unlikely to come in contact with feral zoonoses.

The information about *Ae. albopictus* presented in this document portrays a very complex species. Its ability to harbor indigenous arboviruses has been demonstrated in the United States, and a wealth of experimental data have reinforced the evidence of its potential role in vectoring human and animal arboviral diseases. Complicating the picture is the catholic feeding behavior of the species, which has been reported feeding not only on small and large mammals, including humans, but also on birds, snakes, and turtles. *Ae. albopictus* can enter into sylvan zoonotic cycles and bring such viruses to man; that is why it is so dangerous. Moreover, unlike swamp and marsh mosquitoes, *Ae. albopictus* breeds close to human habitations.

A very disturbing development is isolation of the eastern equine encephalitis (EEE) virus from *Ae. albopictus* mosquitoes collected at the Polk County Tire Dump in Florida. EEE causes severe and often fatal disease in humans. It is also an important disease of domestic animals and has killed a significant number of animals belonging to endangered species, such as the whooping crane.

Houston (Texas) and Brazilian strains of *Ae. albopictus* have shown susceptibility to experimental oral infection with the four dengue serotypes (Mitchell and Miller, 1990). If *Ae. albopictus* spreads into Central America and the Caribbean, it could add new complexity to the scenario of dengue in the Americas. *Ae. albopictus* breeds in urban, rural, and forested areas in water retained by artificial containers and natural vegetation. It is exophilic and prefers to breed outside human dwellings, which makes it potentially dangerous as a maintenance vector.

Seven years after its discovery in the Americas, *Ae. albopictus* continues to expand its range into new geographical areas. In 1986, 11 states in the United States were reported to be infested; by 1991, 11 additional states were known to have significant populations of *Ae. albopictus*. Similarly, in Brazil infestation was reported in 89 municipalities in 1986; by April 1994, 676 municipalities and three new states—Maranhão, Paraná, and Bahia—had been added to the list of infested areas, indicating a well-established breeding population in the country. In addition, the expansion is not restricted to the Americas. In the last few years, the species has spread rapidly to many communities in northern Italy.

There are still many unanswered questions about *Ae. albopictus* and its relationship to human diseases. For instance, no association of *Ae. albopictus* with arboviral dis-

ease outbreaks has been reported in the Americas. The Ministry of Health of Brazil did not find any evidence associating *Ae. albopictus* with the dengue outbreaks reported during the past five years, but more detailed studies need to be carried out during such events, especially since several of the recent dengue epidemics took place in Brazilian states where *Ae. albopictus* is known to be present. Clearly, such studies can help to resolve many of the enigmas which surround this species in natural settings.

Ae. albopictus is a highly adaptable species. Its evolutionary plasticity is demonstrated by its ability to develop insecticide resistance after only a few generations of laboratory selection. Insecticide selection studies of *Ae. albopictus* strains from the United States indicated unusually high tolerance to malathion, resulting in a resistance ratio of 21 after just six generations (Wesson, 1990). Control efforts in infested areas may be compromised if *Ae. albopictus* develops a resistance trait.

Enzyme electrophoretic studies appear to indicate that gene flow in the introduced populations of the Americas is higher than that found among indigenous populations of Southeast Asia. These observations render indirect evidence of the importance of the tire trade in disseminating introduced populations, and show that interdiction of that trade could prevent the colonization of other areas of the hemisphere.

The potential for the species to spread to other ecosystems in the Americas is real, as demonstrated by the recent reports from northern Mexico and the Dominican Republic. If the trend continues, enlargement of the foci in Brazil, the Dominican Republic, Mexico, and the United States can be expected, along with expansion of the infestation to other countries of the Americas, involvement of *Ae. albopictus* in the dengue cycle, and involvement of the species in transmission of zoonotic arboviroses. Moreover, if *Ae. albopictus* spreads into yellow fever endemic areas of South America, it could act as a bridge vector and bring yellow fever to South American urban centers.

The continuing spread of *Ae. albopictus* to new areas requires the urgent attention of health agencies and the scientific community throughout the Americas.

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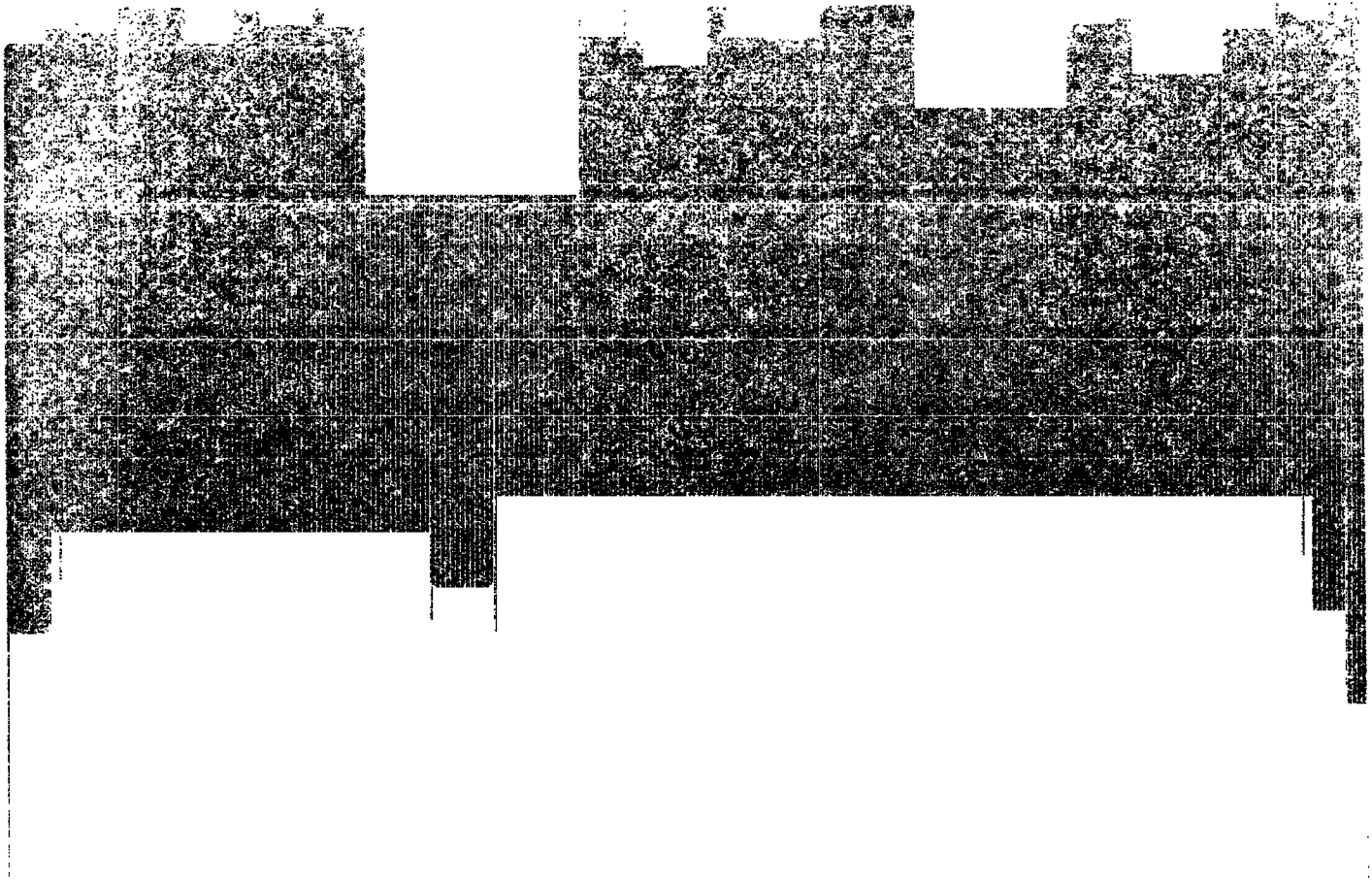

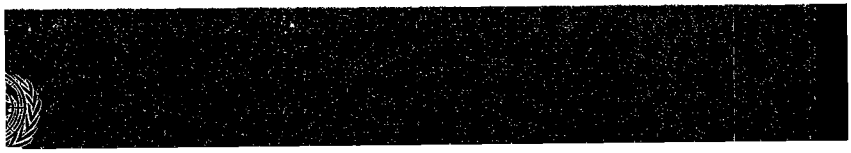

Reprint

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FAGERSTONE, KATHLEEN A., C. A. RAMEY, AND J. KEITH. Mongoose management to protect endangered species in Hawaii. USDA APHIS Denver Wildlife Research Center, Denver, CO 80225-0266 USA.

Mongooses (*Herpestes auropunctatus*) were introduced into Hawaii in 1883 to control introduced rats and now occur on all main islands except Kauai. Whereas mongooses have not limited rat populations, they have limited the productivity of many ground nesting avian species. They have also restricted the recovery of at least 8 species of endangered Hawaiian birds by consuming both their eggs and young. The Denver Wildlife Research Center (DWRC) began investigations in Hawaii in 1984 to develop a management tool for mongoose control. Studies of mongoose biology and toxicology revealed an extreme susceptibility to the anticoagulant diphacinone. Using DWRC data, Bell Laboratories, Inc. obtained a state registration in 1991 for use of diphacinone to control mongoose in bird nesting areas.