

# INVASIONS BY INSECT VECTORS OF HUMAN DISEASE

---

L. Philip Lounibos

University of Florida, Florida Medical Entomology Laboratory, Vero Beach, Florida  
32962; e-mail: Lounibos@ufl.edu

**Key Words** biogeography, establishment, medical entomology, spread, transport

■ **Abstract** Nonindigenous vectors that arrive, establish, and spread in new areas have fomented throughout recorded history epidemics of human diseases such as malaria, yellow fever, typhus, and plague. Although some vagile vectors, such as adults of black flies, biting midges, and tsetse flies, have dispersed into new habitats by flight or wind, human-aided transport is responsible for the arrival and spread of most invasive vectors, such as anthropophilic fleas, lice, kissing bugs, and mosquitoes. From the fifteenth century to the present, successive waves of invasion of the vector mosquitoes *Aedes aegypti*, the *Culex pipiens* Complex, and, most recently, *Aedes albopictus* have been facilitated by worldwide ship transport. Aircraft have been comparatively unimportant for the transport of mosquito invaders. Mosquito species that occupy transportable container habitats, such as water-holding automobile tires, have been especially successful as recent invaders. Propagule pressure, previous success, and adaptations to human habits appear to favor successful invasions by vectors.

## CONTENTS

INTRODUCTION AND DEFINITIONS .....	234
DISEASE OUTBREAKS FOMENTED BY VECTOR INVASIONS .....	235
<i>Aedes aegypti</i> , Yellow Fever, and Dengue .....	235
Epidemic Malaria and Invasive <i>Anopheles</i> .....	236
Bubonic Plague and the Oriental Rat Flea .....	238
INVASIVE VECTOR GROUPS OF THE TWENTIETH CENTURY .....	239
Mosquitoes (Especially Container Occupants) .....	239
Other Vector Diptera .....	241
Kissing Bugs .....	241
Fleas and Lice .....	242
TRANSPORT OF VECTORS ON AIRCRAFT .....	243
MOSQUITO INVASIONS OF PACIFIC ISLANDS .....	244
Hawaii .....	244
Guam .....	244
Australia .....	245
New Zealand .....	246

INVASIONS BY <i>Aedes albopictus</i> .....	246
Arrivals and Establishments .....	246
Spread .....	247
Population Genetics .....	247
Competitive Exclusion .....	249
Evolution of Diapause .....	250
Arboviruses .....	250
<i>Aedes japonicus</i> IN THE UNITED STATES .....	251
THE TENS RULE OF WILLIAMSON AND MOSQUITO INVASIONS .....	251
DETERMINANTS OF INVASION SUCCESS .....	252
INVASION BIOLOGY AND VECTOR CONTROL .....	254
FUTURE DIRECTIONS AND NEEDS .....	254

## INTRODUCTION AND DEFINITIONS

Most observers would agree that Elton's landmark book, *The Ecology of Invasions by Animals and Plants* (49), established the field of invasion biology as a scientific discipline, particularly in light of the increasing incidence of human-assisted dispersal of nonindigenous species. Research in the 1980s organized by the Scientific Committee on Problems of the Environment, part of the International Council of Scientific Unions, documented the extent of plant and animal invasions in specific geographic areas (e.g., 42, 70, 109, 124) and provided a framework for interpreting why certain species and areas are more susceptible than others to invasion (e.g., 65, 88, 95). In the past decade, increasing awareness of the biotic and economic consequences of invasive species stimulated a proliferation of books on case histories (118), geographic and global perspectives and consequences (32, 44, 125, 187), and theory and practice (182, 219); reports and special issues of journals (23, 93, 110), and a new journal (24) confirm the importance of the new discipline. Although possible impacts of nonindigenous mosquito species have been addressed in some of these compilations (33, 57, 206), invasion biology has largely not intersected with that of medical entomology, despite many historical examples of human-aided dispersal of disease vectors.

The term vector is applied to an organism that transfers a pathogen from one host to another (2). This review is limited to invasions of insect vectors of human diseases, although some pathogens carried by the same blood-sucking insects may affect other vertebrate hosts.

Three essential stages—arrival, establishment, and spread—characterize a biological invasion (219). A recent proposal recommends that nonindigenous invaders should be distinguished from colonizers based on impact (39). Accordingly, only a species with great impact on its new environment should be characterized as invasive. However, the impact criterion is highly subjective and depends on scale and personal values (37). Therefore, a more suitable criterion of an invasive species, besides its novelty in a new environment, is spread, measurable as population growth and distance dispersed (37, 159).

Because of lack of consensus of their use, other terms from the literature, such as alien (35), exotic (66), imported (221), nonnative and colonizer (39), will be avoided. Nonindigenous (151) is applied here to the occurrence of species beyond their native range. This review considers invasive vectors as those that satisfy the biogeographic and spread criteria. Some invasive species are unlikely, based on their biology, to become vectors of human pathogens but are nonetheless included in this review because they are in blood-sucking vector groups, such as mosquitoes, and because changes in their behavior in new habitats are unpredictable. After documenting the extent of vector invasions, I try to integrate some developments of invasion biology, culled from results on nonvector pests, especially plants (219), with observations on invasions of medically important insects. Whereas most previous concerns and implications of invasive species are in areas of biodiversity, conservation, ecosystem disruption, and economic losses (147, 151, 206), invasive vectors affect human health by altering patterns and frequency of disease transmission.

This review is not organized systematically by taxon, geography, or disease, but is rather an eclectic sampling of what is known and interesting about vector invasions. Useful records of vector invasions are not available for many areas of the world, and literature prior to the twentieth century is often anecdotal or inadequate for inferences about invasion processes. For some vector groups or vector-borne diseases covered sparsely or not at all in this review, evidence for invasiveness was weak or poorly documented.

## DISEASE OUTBREAKS FOMENTED BY VECTOR INVASIONS

### *Aedes aegypti*, Yellow Fever, and Dengue

*Aedes aegypti*, the so-called yellow fever mosquito, is believed to have migrated from West Africa to the New World in the fifteenth through seventeenth centuries aboard slave ships (29). Alternatively or additionally, *Ae. aegypti* may have first invaded Portugal and Spain before reaching the Western Hemisphere on European ships (197). In either case, the evolution of domestic traits in an originally feral species (197) was crucial for enabling *Ae. aegypti* to occupy and flourish in water storage jars in the holds of these sailing vessels.

Yellow fever was absent from urban settlements in the New World until the arrival of *Ae. aegypti*, the only known vector of urban epidemics of this disease (199). The first clearly documented New World epidemic of yellow fever occurred in the Yucatan in 1648 (119), although it is thought to have appeared in Haiti as early as 1495 (30). Throughout the seventeenth through nineteenth centuries, yellow fever ravaged seaports on the Atlantic Coast, as far north as Philadelphia and New York (199). Presumably the yellow fever virus was being reintroduced by passengers, especially African slaves, on these ships.

In tropical and mild temperate regions of the Americas, *Ae. aegypti* became established and spread into the interior, whereas in the northeastern United States,

where this species was unlikely to overwinter, new arrivals on ships may have vectored the yellow fever epidemics. *Ae. aegypti* was reduced in abundance and distribution, but not eliminated, by an intensive eradication scheme in the 1950s and 1960s (190). Currently the species is widespread in the Americas, where reinfestations after the failed eradication scheme are associated with the reemergence of dengue and the appearance of dengue hemorrhagic fever (72). In North America its distribution receded in the 1990s concomitant with the spread of *Aedes albopictus* in the southeastern United States (80, 120, 143, 145a).

In tropical Asia, *Ae. aegypti* is presumed to have arrived and established later, based on the absence of urban dengue in this region until late in the nineteenth century (189). The more recent dispersal of *Ae. aegypti* in the Oriental region is supported by comparatively low genetic diversity in tropical Asian populations of this species (197).

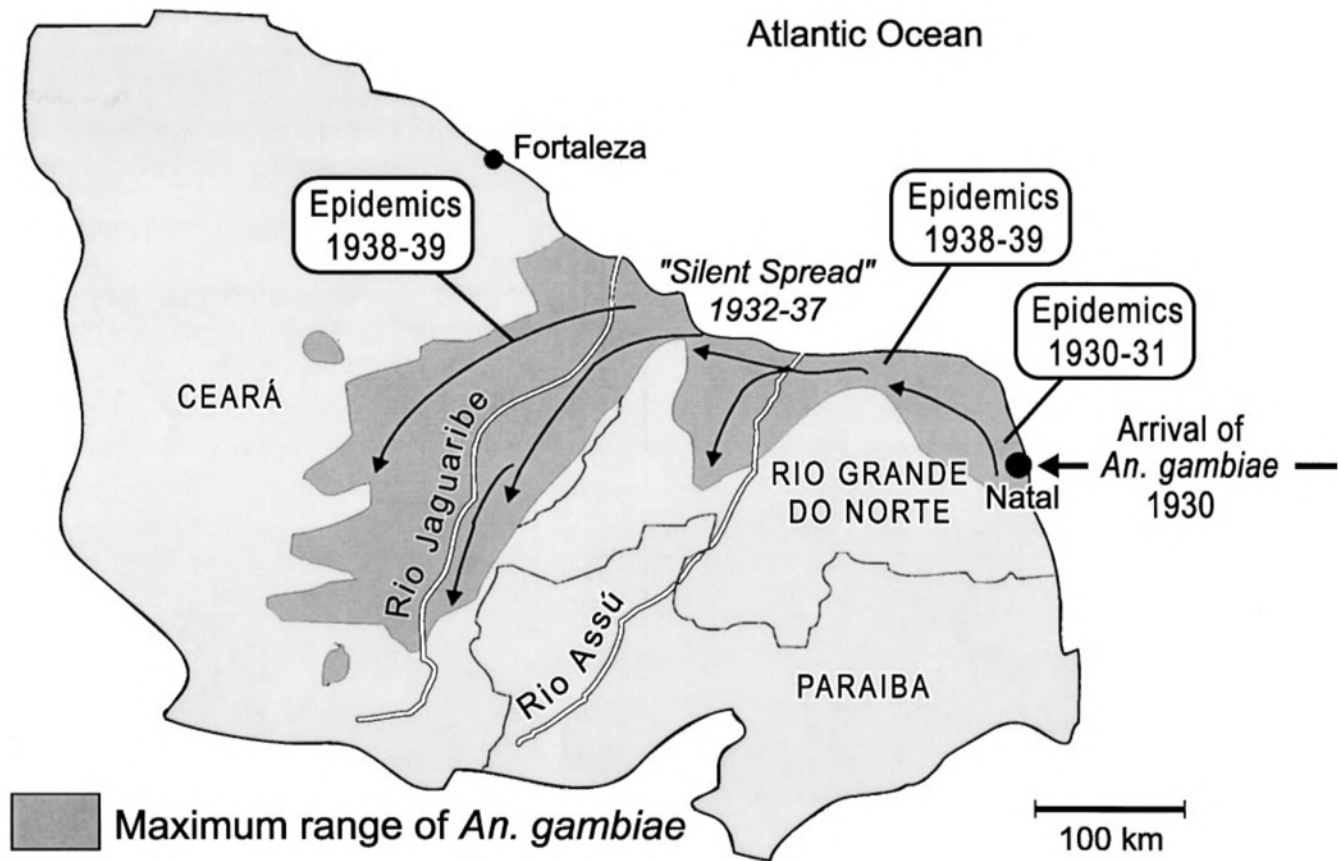
### Epidemic Malaria and Invasive *Anopheles*

The arrival from West Africa in 1930 and establishment and spread into northeastern Brazil of the African malaria vector *Anopheles gambiae* s.l. rivals the introduction of *Ae. aegypti* into the New World for epidemiological impact (191). Larvae or adults of this anopheline are believed to have traveled by air or fast passenger ship from Dakar, Senegal, to Natal, Brazil (153), where the first malaria epidemic attributable to *An. gambiae* s.l. occurred in March–May, 1930. Although malaria was endemic in northeastern Brazil, the native anopheline vectors were inefficient transmitters compared with the highly anthropophilic and endophilic (= house entering) *An. gambiae* s.l. (26, 40).

At the time of its invasion into Brazil (1930–1941), *An. gambiae* was not recognized as a species complex, which consists currently of six closely related named species (62). Of the two members of this complex known as efficient malaria vectors, *An. gambiae* s.s. and *Anopheles arabiensis*, the adaptation of the invader to the dry northeast of Brazil is more consistent with the habits of *An. arabiensis* in the African Sahel region. Intolerance of the Brazilian invader to salt (25) rules out the halophilic species of this complex, *Anopheles merus* and *Anopheles melas*.

Although insecticide treatments eradicated *An. gambiae* s.l. by 1932 in Natal, the invading species escaped and spread outside the city limits (191). In the so-called silent years, the invader spread west, then south (Figure 1), especially along water courses. Then a malaria epidemic that rivaled “the worst outbreaks described in the literature of this disease” (191) occurred in 1938, with mortalities ranging from 10–25%. Such high mortality rates had also occurred on the island of Mauritius in 1866–1867 when accidentally introduced *An. gambiae* s.l. also

**Figure 1** The arrival and spread, especially along river courses, of *Anopheles gambiae*, in northeastern Brazil in the 1930s and associated malaria epidemics. Information derived from Soper & Wilson (191). Ceará, Rio Grande do Norte, and Paraíba are state names.



fomented malaria epidemics (167). In both Mauritius and Brazil, the invasion of *An. gambiae* s.l. changed malaria transmission from endemic to epidemic.

Field observations indicated that the spread of *An. gambiae* during 1930–1937 occurred primarily by infiltration, i.e., movement from one habitat to another by natural dispersal (191). However, long-distance dispersal in 1939–1940 may have been assisted by car, train, or boat. Preferred larval habitats in this arid region were small temporary pools, borrow pits, and shallow wells (caçimbas) dug for drinking water (25).

Concentrations of this species in discrete areas, especially during the dry season, facilitated the successful massive eradication scheme led by the Rockefeller Foundation, which treated larval habitats with the highly toxic Paris green (191). Coupled with house spraying with pyrethrum, the African invader was eliminated, without DDT, only 19 months after the eradication campaign began (40). As soon as *An. gambiae* s.l. disappeared from northeastern Brazil, malaria incidence dropped precipitously (26).

*Anopheles darlingi*, the most efficient malaria vector native to the New World, is the principal transmitter of this disease in the Central Amazon region (106). Prior to the 1990s, this species was sparsely distributed in the Upper Amazon region of Peru (22) and absent from the Iquitos region as recently as 1991 (137). However, sometime early in the past decade, this species appeared in abundance in the vicinity of Iquitos and became the primary vector of epidemic malaria (51), with more than 130,000 registered cases in 1997 among a population of less than four million persons (5).

Although the mode of range expansion of *An. darlingi* into the Loreto (Iquitos) Region is unknown, one speculation is that larvae were transported by boats with tropical fish, which are cultivated locally for export and sale in the aquarium trade. Artificial ponds excavated for fish culture, so-called piscigranjas, are used as larval habitats by *An. darlingi* in the Iquitos region (106) in addition to the littoral riverine and backwater habitats occupied by this species in its native range (111, 169).

## Bubonic Plague and the Oriental Rat Flea

The plague bacillus, responsible for the Black Death of the Middle Ages, is transmitted to humans from infected rodents, often rats, by flea bites, usually from the Oriental rat flea *Xenopsylla cheopis* (102). Three pandemics of bubonic plague—from the sixth to eighth centuries AD, during medieval times, and from late-nineteenth into early-twentieth century—are estimated to have killed more than 200 million persons (46). The worldwide pattern of outbreaks in ports during the last pandemic suggests that the disease was probably introduced from infected Norway rats that disembarked from sailing ships or freight vessels accompanied by *X. cheopis* and other flea species (K.L. Gage, personal communication). During that pandemic, plague began in inland China and reached Chinese port cities in 1894, from which at the turn of the century it was disseminated by ships and erupted in epidemic form at major international ports such as San Francisco, Asuncion, Rio de Janeiro, Brisbane, Sydney, and Bombay (46).

Insofar as the cosmopolitan *X. cheopis* was probably already present in these ports, the arrival of infected Oriental rat fleas on ships does not constitute an invasion in the strict sense. However, in light of the drastic epidemiological consequences of introduced fleas infected with plague, this example is included in the review. It is generally believed that the plague epidemic in San Francisco in 1899 led to the permanent establishment of plague as an endemic disease of wild rodents in the western United States (103).

## INVASIVE VECTOR GROUPS OF THE TWENTIETH CENTURY

### Mosquitoes (Especially Container Occupants)

The extensive mosquito literature includes records of long-distance dispersal of adults, unassisted by humans, far from their larval habitats (e.g., 155, 200). On occasion, such dispersals have led to short-term colonizations that temporarily extended the range of a species, such as inland-inhabiting populations of the salt marsh mosquitoes, *Aedes taeniorhynchus* and *Aedes sollicitans* (94, 155).

Most recent successful invasions of mosquitoes have resulted from human transport of immature stages. Mosquitoes that occupy small water bodies, especially container habitats, in their larval and pupal stages are responsible for the most notable invasions and range expansions in the United States (Table 1). The highly publicized invasion of the Asian tiger mosquito *Aedes albopictus* (33) and the more recent establishment and spread of *Aedes japonicus* in the United States (149) are considered subsequently in a separate section of this review. Both of these species are believed to have hitchhiked to their ports of arrival in shipments of used tires (34, 149, 156), recognized since World War II for their potential in mosquito transport (154).

A major range expansion of the native mosquito *Aedes atropalpus* in the United States is also attributable to the recent adaptation of this species to water-holding automobile tires (12). Prior to 1972 this larval inhabitant of lotic and lentic rock holes was unknown in the states of Ohio, Indiana, and Illinois (222). However, collections from discarded tires in the late 1970s and 1980s extended the range of this species into these midwestern states (9, 158). Its more recent establishment in Nebraska (87) was probably also facilitated by tire transport. Now, *Ae. atropalpus* occurs in tires in parts of its original range, such as Kentucky, New York, and Connecticut, where it was formerly confined to rock holes (3, 31, 212). After reaching Europe in tire shipments, this species has also become established in Italy (163).

*Aedes bahamensis* was first discovered in the United States in 1986 from light and oviposition trap collections in southern Florida (146). It was probably transported from the Bahamas, where it is a common peridomestic mosquito in used tires, a preferred larval habitat in Florida (145). In the 15 years since its original detection, *Ae. bahamensis* has not spread outside Broward and Miami-Dade counties in Florida (G.F. O'Meara, unpublished results).

**TABLE 1** Twentieth century invasions by container-inhabiting mosquitoes into the United States

Species	Regions		Transport	Date	Key reference
	Donor	Recipient			
<i>Aedes albopictus</i>	Japan	Texas	Tires	1985	77
<i>Aedes atropapulus</i>	Eastern United States	Illinois, Indiana, Nebraska, Ohio	Tires	1970–1980	12
<i>Aedes bahamensis</i>	Bahamas	South Florida	Tires	1986	145
<i>Aedes japonicus</i>	Japan	Connecticut, New Jersey, New York	Tires	1998	149
<i>Aedes togoi</i>	Asia	Pacific NW	Ships	1940–1950	11
<i>Culex biscaynensis</i>	Caribbean (?) <sup>a</sup>	South Florida	Bromeliads	?	142
<i>Toxorhynchites brevipalpis</i>	E. Africa	Hawaii	Biocontrol	1950s	194
<i>Toxorhynchites amboinensis</i>	Pacific region	Hawaii	Biocontrol	1950s	194
<i>Wyeomyia mitchellii</i>	Caribbean or Florida	Hawaii	Bromeliads	1970s	183

<sup>a</sup>It remains unclear whether this recently described species (223) was introduced in exotic bromeliads to south Florida or is, rather, an indigenous species that had previously escaped recognition despite intensive mosquito collecting in the state.

The maritime rockpool mosquito *Aedes togoi* has a tropical to subarctic distribution in the Oriental region (192) and in the New World occurs along a 250–300 km stretch of the coastlines of British Columbia and Washington state (11). Records of halophilic *Ae. togoi* larvae in tire shipments (34), bilges (83), and an adult female on board a ship (17) in Japan suggest that the North American founders may have reached the Pacific Northwest via shipping from Asia sometime before the late 1960s when the first larvae were recovered from rock holes in Vancouver (11).

*Wyeomyia mitchellii*, whose larvae inhabit water-containing plant axils, was discovered in Hawaii in 1979 (183). The immature stages of this species probably reached the Hawaiian Islands in the axils of ornamental bromeliads transported from Florida or the West Indies, where this species is native (183). Transport in the axils of exotic bromeliads may also explain the presence in southernmost Florida of a newly described and narrowly distributed species, *Culex biscaynensis* (142, 223). Known only from suburban Miami-Dade County in the vicinity of Fairchild Tropical Gardens, it is presently unclear whether this species was introduced recently from elsewhere in the Caribbean or is indigenous to south Florida, where it was first detected only recently (Table 1).



Two species of nonbiting mosquitoes of the genus *Toxorhynchites* became established in Hawaii (194) following their releases in the early 1950s for the biological control of *Ae. albopictus* by their predatory larvae (Table 1). Although nonindigenous species of *Toxorhynchites* were also released elsewhere, such as in the city of New Orleans (52), for the control of container mosquito pests, they did not survive temperate winters in the continental United States.

## Other Vector Diptera

**SIMULIIDAE** Long-distance aerial dispersal is characteristic of certain species of black flies, known to travel 150–200 km without human assistance (58, 60). For tropical vectors of onchocerciasis, such as *Simulium dammosum* s.s., wind-aided dispersal associated with the passage of the InterTropical Convergence Zone propels black fly adults to areas where rain is likely to fall and rivers, the larval habitat, flow (60). On a practical level, this long-distance dispersal caused the World Bank's Onchocerciasis Control Program, plagued by reinvasions from nontreated areas, to reevaluate and extend the boundaries of its treatment areas in West Africa (207). The long flight range of black fly vectors of disease may also be epidemiologically significant because infections acquired early in the adult fly's life may be transported over vast distances (60).

**CERATOPOGONIDAE** Biting midges of this family transmit the nematode  *Mansonella ozzardi* and Oropouche fever virus to humans, although they are more important as vectors of domestic animal diseases. Wind-aided dispersal of *Culicoides* vectors has been documented as a mechanism of transport of such animal viral diseases as bluetongue, African horse sickness, and Douglas fever (18, 131, 179). *Culicoides belkeni*, a pest species indigenous to Tahiti, successfully invaded other Polynesian islands after transport on aircraft (150).

**GLOSSINIDAE** Tsetse flies, like Ceratopogonidae, are better known as disease vectors to domestic animals but remain locally important in Africa as transmitters of human sleeping sickness. As for black flies, some evidence for invasiveness comes from reinfestations of areas from which tsetse were eradicated. The West African island of Principe was freed of *Glossina palpalis* for approximately 40 years before the species was reintroduced by ship or plane from Fernando Po, about 200 km distant (6).

Human alterations of the landscape may promote range extensions of tsetse species, such as hedgerow plantings in the Nyanza District of Kenya that led to local expansions of the distribution of *G. palpalis* (134). The *morsitans* group of *Glossina* are known for spreading into countryside from which they were previously absent at rates up to 11.3 km per year (134).

## Kissing Bugs

Schofield (176) has provided evidence for recent, host-associated range expansions of species among the triatomine vectors of Chagas disease. The best documentation

is for the human-aided spread of *Triatoma infestans*, the most important vector of *Trypanosoma cruzi* in South America. Domestication of this bug species is presumed to be pre-Columbian, whereafter dispersal followed pre-Inca tribal migrations from native Bolivia to southern Peru and northern Chile (176). Early in the 1900s, *T. infestans* accompanied migrant workers across Paraguay and Argentina to coffee farms in the vicinity of São Paulo, Brazil (176). Later, following the clearing of Brazilian coastal forests, this vector species colonized more southerly regions of the country (161) and, independently, northeastern Brazil (8). These changes in distribution of *T. infestans* in the past century have been associated with outbreaks of acute Chagas disease in Brazil (8). Once *T. infestans* had been passively transported into an area, probably among domestic effects, it may have actively dispersed among houses by flights up to 200 m (178).

*Triatoma rubrofasciata*, a nonvector relative of *T. infestans*, occurs in both the New World and southeast Asia. Schofield (176) postulates that Old World populations, which are confined mainly to port cities, were derived from New World transport during the seventeenth through twentieth centuries with ship rats, a principal host of *T. rubrofasciata*.

*Rhodnius prolixus*, the Chagas disease vector species made famous by insect physiologists (215), has a disjunct distribution with a gap between Central American and Venezuelan/Colombian populations (45). Early researchers hypothesized that nymphs and eggs of this species were transported phoretically from South to Central America in the plumage of storks, which may harbor *R. prolixus* in nests and routinely migrate between these regions (59). However, other investigators (177, 224) favor a hypothesis that Central American *R. prolixus* are derived from an accidental release in El Salvador of laboratory-reared insects originally collected in Venezuela (138). These escapees and their descendants are presumed to have disseminated to other Central American countries by passive transport among immigrants (177). A recent establishment of this species west of Rio de Janeiro, Brazil, is also suspected of having resulted from a laboratory escape (152).

## Fleas and Lice

Various species of fleas besides *X. cheopis* transmit plague (102); some flea species, such as the dog *Ctenocephalides canis*, cat *Ctenocephalides felis*, and human flea *Pulex irritans*, are cosmopolitan in distribution. Although human migrations undoubtedly promoted the range expansions that led to the contemporary distributions of these species, the historical timing and direction of these range extensions are not known (e.g., 82, 101).

Phoretic transport of the human body louse on migrating troops was responsible for the spread of typhus, which erupted in epidemic form during wars from the Middle Ages through World War II, when delousing with DDT interrupted transmission (30). Although human lice may have been present in an uninfected region before the arrival of troops, the massive influx of abundant and infected *Pediculus humanus* was the immediate cause of typhus epidemics during wartime.

## TRANSPORT OF VECTORS ON AIRCRAFT

Airplanes were recognized as a mechanism of transport of undesirable insects, especially mosquitoes, not long after the implementation of commercial, transcontinental flights (69, 196). Fumigation, or "disinsectization" of aircraft arriving from the tropics, as well as insect control at receiving airports, were recommended to prevent the establishment of undesirable pests and disease vectors that might hitchhike aboard flights (214, 216). The malaria epidemics in northeastern Brazil vectored by *An. gambiae*, possibly transported on aircraft from Africa (191), heightened concerns about the dangerous consequences of vector arrivals aboard international flights. Mosquitoes representing five genera were identified from inspections of aircraft arriving in northeastern Brazil from Africa in 1941–1942 (191). Whitfield (214) provided a 13-page "world list" of all insects identified from captures in commercial aircraft through the 1930s and cautioned that catastrophic epidemics of malaria or yellow fever were inevitable unless improved precautions were undertaken to minimize mosquito transport via international flights.

Given such dire warnings and the ever-increasing volume of air traffic, it is perhaps surprising that, in the sixty-plus years since *An. gambiae* was eradicated from Brazil, no further disease epidemics have been associated with the arrival of vectors via aircraft. However, both dengue and malaria have since been transmitted on Pacific islands by mosquito species that probably arrived on military airplanes, and subsequently became established, during and after World War II (188). Despite fears about the international transport of *Ae. aegypti* (41), this notorious disease vector has been detected relatively infrequently aboard aircraft (41, 84). Monitoring between 1948 and 1960 of international mosquito arrivals at six airports in the continental United States and Hawaii detected 20 species nonindigenous to the continental United States and 31 nonindigenous to Hawaii (50, 84). None of these arrivals via aircraft became established.

Mosquitoes can survive moderately high atmospheric pressures aboard aircraft (96) and can be transported alive between international destinations even in wheel bays (170). Properly conducted insecticide applications, either on the ground or in-flight, are demonstrably effective in reducing the risk of insect imports by aircraft (171, 172). However, assiduous "disinsection" (the more modern term for fumigation of aircraft) is rare (98) and, thus, is probably not responsible for the lack of establishment success of the majority of vectors arriving on airplanes.

Although nonindigenous mosquito species arriving on aircraft rarely become established, irregular cases of insect-borne diseases unknown to a host country implicate transmission by vectors arriving on international flights. The best known example is "airport malaria," infection with malaria, especially *Plasmodium falciparum*, among persons who live near international airports but have not themselves visited malaria-endemic countries. In continental Europe, where endemic malaria was eradicated by the end of World War II (75), such cases occurred, especially in summer months, in the vicinity of international airports in Belgium, England, France, Italy, the Netherlands, Spain, and Switzerland (16, 36, 81, 164, 188). There

is even evidence for malaria transmission on board an international flight (213). It is generally believed that native European anophelines are refractory to transmitting *P. falciparum* (160), precluding their involvement in these cases of airport malaria, although this assumption has recently been questioned (112).

## MOSQUITO INVASIONS OF PACIFIC ISLANDS

Elton (49) called attention to the susceptibility of remote islands to invasive species, noting that 420/1100 of the insects catalogued for Hawaii at the time of his book were nonindigenous. Although Simberloff (186) pointed out that "every sort of havoc wrought by non-indigenous species on islands can be found on the mainland as well," the fates of invasive mosquitoes on selected islands in the Pacific are worthy of attention because of (a) depauperate endemic faunas on some islands; (b) high propagule (arrival) pressure by sea and air; and (c) active vigilance and good faunal records.

### Hawaii

All five species of biting mosquitoes currently known from Hawaii are nonindigenous (89, 183). *Aedes albopictus* is believed to have arrived by boat from elsewhere in the Oriental region sometime in the 1890s (89). The cosmopolitan *Aedes vexans*, believed to have been transported, possibly aboard aircraft, from more westerly Pacific islands was first detected in 1962 (90). *Ae. aegypti* formerly occurred in Oahu but was eradicated in the 1950s (132).

The first mosquito species to have invaded Hawaii was *Culex quinquefasciatus*, believed to have arrived on a ship from Mexico as early as 1826 (20, 43). This mosquito species is the unique local vector of *Plasmodium relictum*, the causative agent of avian malaria that contributed to the endangerment and extinction of native species of Hawaiian birds (204). Fonseca et al. (54) examined microsatellite markers and mtDNA haplotypes of *Cx. quinquefasciatus* from 38 collection sites on the four main Hawaiian Islands. This first application of DNA markers to trace vector invasions demonstrated genetic isolation of this mosquito species among islands and bottlenecks among populations on the Big Island of Hawaii, as well as evidence for multiple introductions.

### Guam

In one of the most comprehensive studies of an invasive fauna, Ward (208) described the biogeographic origins of all mosquito species known to occur on the island of Guam, located 5000 km to the west of Hawaii. Only 7 of Guam's 24 species are endemic, the majority of the 17 nonindigenous species having become established after World War II. Only three introduced mosquito species, *Ae. aegypti*, *Cx. quinquefasciatus*, and *Ae. vexans*, were present on the island in the early 1900s, and *Ae. aegypti* was eradicated late in the 1940s after vectoring frequent outbreaks of dengue during World War II (208).

The remaining 14 nonindigenous mosquitoes include five species of *Anopheles*, four *Culex*, two *Aedes*, and one each from the genera *Armigeres*, *Mansonia*, and *Aedeomyia*. Most of these species occur in the Oriental region, which is the most probable source of their introductions. The absence of invasive mosquitoes from the New World is believed attributable to intensive disinsection of aircraft arriving via Hawaii (208).

Based on intensive post-war collection records, most invading mosquitoes reached Guam between 1960–1969 (five species) and 1970–1979 (seven species). These arrivals were facilitated by increases in international air traffic, including inter-island transports such as Air Nauru. Several of the introduced species, such as *Mansonia uniformis* and *Aedeomyia casticata*, whose larvae are associated with floating aquatic macrophytes, might have arrived as larvae amidst plants transported by seaplane.

After the eradication of *Ae. aegypti*, episodes of diseases transmitted by invasive mosquitoes have been rare on Guam. Dengue was believed to have been transmitted by *Ae. albopictus* in 1975 (188), and a few autochthonous cases of malaria may have been vectored by *Anopheles indefinitus* (208), both of which reached Guam in the 1940s with U.S. or Japanese forces.

## Australia

Out of 242 mosquito species recognized in Australia, only 4 have invaded from abroad (113, 128, 211). The now cosmopolitan *Ae. aegypti* and *Cx. quinquefasciatus* arrived first, with or shortly after the colonial First Fleet (113), and subsequently vectored dengue and filariasis, respectively, in Queensland (63). *Culex molestus*, a member of the *Cx. pipiens* Complex that includes *Cx. quinquefasciatus*, was introduced from the Palearctic Region into Victoria (New South Wales) after World War II (113).

*Culex gelidus*, the first successful invader in more than 50 years, was identified in 1999 from collections near the Brisbane (Queensland) airport (128). Although this small population of *Cx. gelidus* was exterminated, subsequent surveillance for this species showed it to be widely distributed in New Territories (211), and it is now also known in Western Territories (R.C. Russell, personal communication). Examinations of undetermined voucher specimens in Australian collections revealed that *Cx. gelidus* arrived, probably from Indonesia or Papua New Guinea, and became established as early as 1996 (211).

Given northern Australia's close proximity to tropical countries with diverse mosquito faunas, and its favorable climate for invasive tropical organisms, the presence of only four invasive mosquito species is surprising. Australia was the first country to apply quarantine code to aircraft (173); disinsection of aircraft, airport "sanitation," and inspection and fumigation of vessels arriving by sea may have prevented the establishment of a greater number of invasive mosquito species (173; R.C. Russell, personal communication). Despite frequent international arrivals from malarious areas, only a single case of airport malaria has been recorded in Australia (173).

**TABLE 2** Total culicid fauna and incidence of biting, invasive mosquitoes in two mainland and four island areas

Area	Established invasives			Most recent detection	Key citations
	Total culicid spp.	No.	% Total		
Continental United States	174	8	4.6	1998	Table 1; 38, 166
Italy	54	2	3.7	1996	162, 195
Hawaii	5 <sup>a</sup>	5	100.0	1979	89, 183
Guam	24	17	70.8	1979	208
New Zealand	17	4	23.5	1998	10, 78, 139
Australia	242	4	0.8	1999	113, 211

<sup>a</sup>Excludes nonbiting *Toxorhynchites* spp. Listed in Table 1.

## New Zealand

Compared with neighboring Australia, New Zealand has a depauperate native mosquito fauna composed of only 13 species (10). However, four nonnative species, a number equal to Australia's invasive mosquito species, brings this nation's total mosquito fauna to 17 (Table 2). Three of these, *Aedes australis*, *Aedes notoscriptus*, and *Aedes camptorhynchus*, are imports from Australia (78, 150; G. Browne, personal communication). Although the first two of these are believed to have arrived via ships early in the twentieth century (210), the salt-marsh species *Ae. camptorhynchus* was first detected only in December of 1998 and is also believed to have been ship-borne (139). The only invasive species shared by New Zealand and Australia, *Cx. quinquefasciatus*, supposedly reached New Zealand prior to 1848 aboard sailing vessels (210).

Owing to its sparse native mosquito fauna, isolation, and absence of tropical climates, no mosquito-borne diseases are known to occur in New Zealand (210). However, during the course of increased surveillance in the 1990s, the potential arbovirus vectors *Ae. albopictus* and *Ae. japonicus* have been intercepted in tire shipments from the Oriental region (78, 99).

## INVASIONS BY *AEDES ALBOPICTUS*

### Arrivals and Establishments

Widespread invasions by the Asian tiger mosquito *Ae. albopictus* in the past two decades, facilitated by tire shipments, are regarded as the "third wave" of human-aided dispersal of mosquito vectors of human disease, following the previous cosmopolitan spread of *Ae. aegypti* and the *Cx. pipiens* Complex (21). The native range of *Ae. albopictus* is centered in the Oriental region and India (76) but extends

west to the African island nations of Mauritius, the Seychelles, and Madagascar (116). In the hundred years preceding its most recent diaspora (33), *Ae. albopictus* had spread to Hawaii, Guam, and other Pacific islands (76, 89, 208).

Before its establishment in the vicinity of Houston, Texas in 1985 (193), *Ae. albopictus* had been detected previously in tire shipments at North American ports (47) and in a cemetery in Tennessee (157). Based on diapause responses of U.S. populations founded shortly after its arrival, Hawley et al. (77) deduced that North American *Ae. albopictus* originated from temperate Japan. *Ae. albopictus* that nearly simultaneously colonized southeastern Brazil (55) showed no diapause, suggesting a tropical origin for Brazilian founders (77).

In southern Europe, *Ae. albopictus* was discovered established in Albania in 1979 (1), in Italy in 1990 (174), and in France in 1999 (181). Its puzzling absence from mainland Africa (116) was remedied by the detection of *Ae. albopictus* in Nigeria in 1991 (175). Following its establishment and spread in both the United States and Brazil, the Asian tiger mosquito was recorded from Mexico (86), Argentina (168), Guatemala (141), and Caribbean islands such as Hispanola (148), Cuba (19), and the Caymans (G.F. O'Meara, personal communication). Shipments of used tires have been implicated as the primary dispersal mechanism of this spread (156).

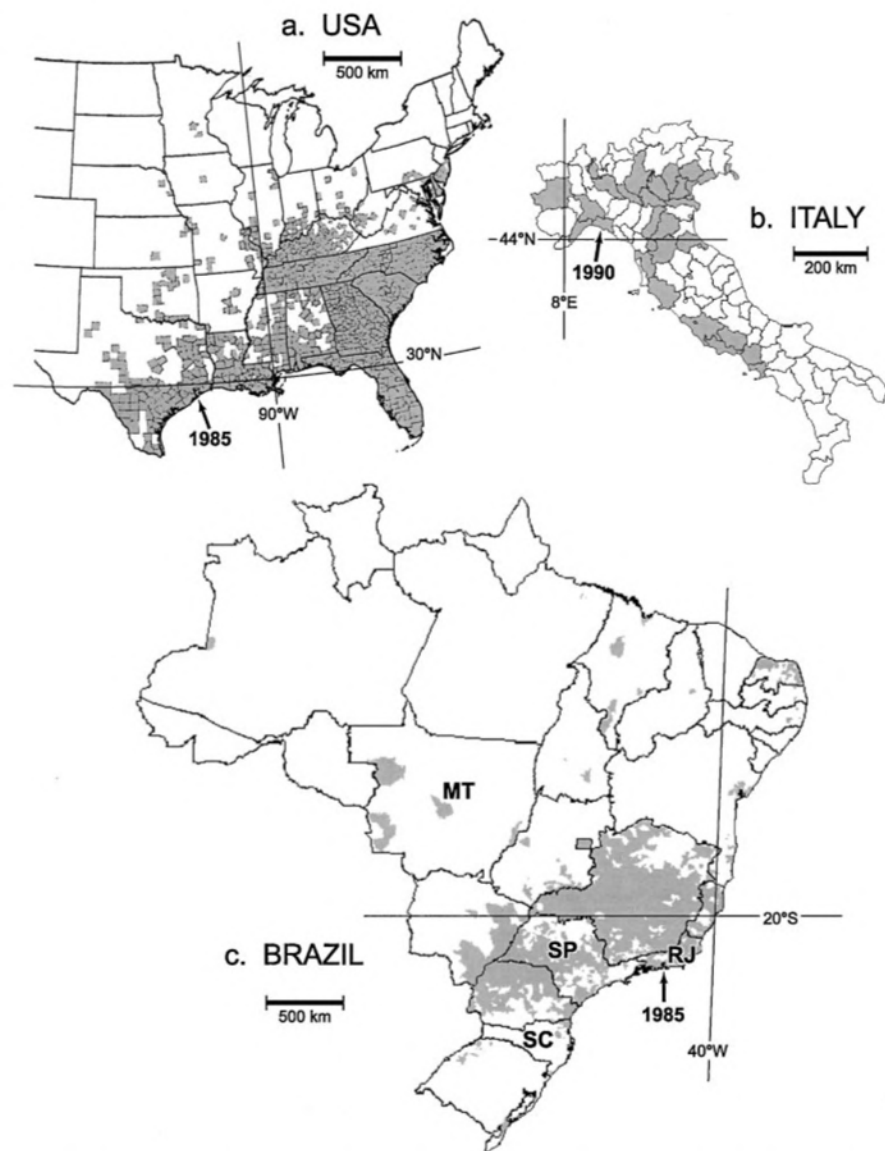
## Spread

The eastward and northward expansion of *Ae. albopictus* in the United States has been carefully documented from state and county surveillance records (126). The northern limits of the species (Figure 2a) correspond approximately to the  $-5^{\circ}\text{C}$  isotherm, as predicted by cold-hardiness studies (136). Despite interceptions at western ports (34), *Ae. albopictus* has not colonized the western United States, possibly because of climatic incompatibilities (209). The species, which entered Florida in 1986 from the temperate north, was established in all Florida's 67 counties by 1994 (143, 144).

Improved surveillance has filled in gaps of a previously reported patchy distribution of *Ae. albopictus* in Italy (162), which now extends from Naples in the south to the northern borders of that country (Figure 2b) (R. Romi, personal communication). The current known distribution of *Ae. albopictus* in Brazil suggests northern, southern, and westward expansion from the site of original infestation in the southeast of that country (Figure 2c) (Fundação Nacional da Saude, unpublished information), although multiple introductions cannot be ruled out. It is not known whether seemingly isolated foci, such as on the northeast coast or in Amazonian regions of Mato Grosso State (Fundação Nacional da Saude, unpublished information), represent a disjunct distribution in that country or, rather, gaps in surveillance.

## Population Genetics

Isozyme analyses conducted shortly after the eastward and northward dispersal of *Ae. albopictus* in the United States were interpreted as indicating rapid local



**Figure 2** Suspected ports of arrival (arrows with years) and recent distributions of *Ae. albopictus* in (a) the United States (modified from 126), (b) Italy (modified from R. Romi, personal communication), and (c) Brazil (modified from Fundação Nacional da Saude, unpublished data, 1999). For Brazil, States referenced in text are indicated by abbreviations: MT, Upper Mato Grosso; SP, São Paulo; RJ, Rio de Janeiro; SC, Santa Catarina. Geographic divisions for the United States are states, and for Italy, provinces.



differentiation (13). Similar patterns of isozyme variation were detected at the heart of its native range in the tropics, suggesting that local genetic differentiation is characteristic of this species (14). A comparable electrophoretic study of Italian *Ae. albopictus* confirmed significant variation in allele frequencies among subpopulations attributable to genetic drift (202). Isozyme patterns were also interpreted as indicating a common geographic origin of *Ae. albopictus* in Brazil and the United States (92), although this conclusion conflicts with distinctive mtDNA profiles in samples from the two countries (12a), a more comprehensive analysis of 27 isozyme loci (L.E. Munstermann, unpublished data), and different diapause responses (77; L.P. Lounibos, unpublished data). An examination of DNA sequences of the mitochondrial ND5 subunit of NADH dehydrogenase showed that Brazilian populations of *Ae. albopictus* harbored private haplotypes not present in samples from the United States (12a).

### Competitive Exclusion

The decline in abundance and widespread disappearance of *Ae. aegypti* in association with the *Ae. albopictus* invasion in the southeastern United States has been well documented (33, 80, 120, 143). Once broadly distributed throughout the Southeast, *Ae. aegypti* is now restricted to urban habitats in southern Texas, Florida, and in New Orleans (145a). Mechanisms proposed to explain the rapid range reduction of the yellow fever mosquito include (a) sterility from interspecific matings with *Ae. albopictus* (133); (b) differential mortality caused by infection of *Ae. aegypti* with *Ascogregarina taiwanensis*, a parasite introduced into the United States with *Ae. albopictus* (33, 130); (c) hatching inhibition of *Ae. aegypti* eggs by larvae of *Ae. albopictus* (48); and (d) superiority of *Ae. albopictus* in larval resource competition (91).

Although earlier laboratory studies, which used protein-rich diets, seemed to show that *Ae. aegypti* was the superior larval competitor (15, 79), Barrera (7) demonstrated superior performance of *Ae. albopictus* when leaf litter, a natural substrate, was used. In a natural Florida woodland where competitive exclusion had recently occurred, Juliano (91) showed that *Ae. albopictus* outcompeted *Ae. aegypti* in resource-limited automobile tires. Although the larval competition hypothesis satisfactorily explains most instances of displacement in the southeastern United States, mechanisms for *Ae. aegypti*'s urban persistence in selected southern states remain unclear (145a).

Based on experiments in laboratory microcosms, Livdahl & Willey (104) predicted that *Ae. albopictus* would exclude the native North American treehole mosquito *Aedes triseriatus* from tire habitats, but not from treeholes. Analyses of pre- and postinvasion larval samples in Florida confirmed coexistence of the two species in treeholes, but with a temporal trend in mean crowding that favors *Ae. albopictus* (107). In Florida, *Ae. triseriatus* was rare in discarded urban or suburban tires even before the arrival of *Ae. albopictus* (107). In South Carolina

*Ae. triseriatus* abundances in oviposition traps decreased after the *Ae. albopictus* invasion in that state (120).

## Evolution of Diapause

Egg diapause is induced in temperate *Ae. albopictus* by exposing female pupae and adults of the preceding generation to short daylengths (76). A high incidence of egg diapause was reported for six populations of *Ae. albopictus* shortly after their establishment in the United States (77). Although Craig (33) claimed that diapause was lost after *Ae. albopictus* adapted to subtropical Florida, populations from that state tested in 1999–2000 all expressed this trait when exposed to short daylengths (10L:14D) at 21°C, with the incidence of diapause decreasing in a north to south geographic cline, ranging from 99% near the Florida-Georgia border (30.5° latitude) to 65% south of Miami (25.5°N latitude) (L.P. Lounibos & R.L. Escher, unpublished data). Conversely in Brazil, where collections in 2000 from Rio de Janeiro and São Paulo states did not respond to diapause-inducing photoperiods, 5–10% of eggs of *Ae. albopictus* from the more southerly and temperate Santa Catarina state (26.9 and 27.7°S latitude) (Figure 2c) entered diapause in response to short daylengths received by their mothers (L.P. Lounibos, R.L. Escher & R. Lourenço-de-Oliveira, unpublished data). Thus, selection for diapause expression since the establishment of *Ae. albopictus* in the two hemispheres has acted in opposite directions to facilitate adaptive evolution from temperate to subtropical habitats in the United States and from tropical to temperate in Brazil.

## Arboviruses

In its native range *Ae. albopictus* is known as a vector of dengue virus, which was isolated from Mexican collections of the species after an epidemic (85). After its invasion of the United States, there was concern for the diverse arboviral zoonoses in which *Ae. albopictus* might participate in its new American environments (121, 127). Wild-caught *Ae. albopictus* females were recovered infected with the highly pathogenic eastern equine encephalitis virus at a tire dump in south Florida located on the edge of a swamp (123). Several other nonpathogenic viruses have been isolated from *Ae. albopictus* collected at other North American localities (56, 74). Recently, LaCrosse encephalitis virus was isolated from field-collected eggs of *Ae. albopictus* in areas of North Carolina and Tennessee where human cases of this disease had recently occurred (61). Risks of arbovirus transmission by *Ae. albopictus* in Europe have been discussed by Mitchell (122).

The high annual incidence of dengue in Brazil, with more than 250,000 cases registered in 1997 (38a), renders it probable that *Ae. albopictus* will play some role in transmission, although the first reported isolate of dengue virus from *Ae. albopictus* in this country (180) is regarded as disputable. A looming concern is that *Ae. albopictus* can be a bridge vector for sylvan yellow fever, which remains common in Brazil (64, 114). Use of abundant epiphytic bromeliads as larval habitats could expose *Ae. albopictus* to the natural reservoirs of yellow fever infection

in arboreal primates (135). Marques et al. (114) discuss other arboviruses that might be vectored by *Ae. albopictus* in Brazil.

## AEDES JAPONICUS IN THE UNITED STATES

In 1998 *Ae. japonicus*, a container-inhabiting mosquito species native to Korea and Japan (198), was detected in light trap collections in New York and New Jersey, which it likely reached in tire shipments (149). Its presumed arrival in tires is supported by detection of this species on several occasions in imported tires intercepted in New Zealand (78, 99). The species was detected independently in 1998 in human biting collections in Connecticut (129), where its immatures now inhabit a wide variety of artificial and natural container habitats (4). The species has also spread westward and inland in Maryland, Pennsylvania, and Ohio (53).

Fonseca et al. (53) compared RAPD profiles and mtDNA haplotypes of *Ae. japonicus* from various sites in Japan and throughout its current range in the United States. Samples from New York, Connecticut, and New Jersey were separable from Pennsylvania and Maryland collections by distinctive DNA profiles. Small sample sizes precluded determination of whether exclusive haplotypes in these two areas were attributable to independent introductions or to rapid genetic divergence caused by founder effects (53). All North American samples bore genetic similarities to some Japanese populations, although the origin of founders could not be determined precisely.

During intensive arbovirus surveillance in the past two years in the northeastern United States, a pool of wild-caught *Ae. japonicus* was detected infected with the recently established West Nile virus (27). The demonstrated ability of this species to be infected by and to transmit West Nile virus (201) indicates that this combination of new pathogen and new vector could become epidemiologically significant in eastern North America.

## THE TENS RULE OF WILLIAMSON AND MOSQUITO INVASIONS

Williamson (217–219) derived a statistical generalization, applicable to a range of invasive plants and animals, that states that approximately 10% of nonindigenous arriving species become established, and of the establishments, about 10% become pests. Exceptions to the “Tens Rule” included crop plants, Hawaiian birds, insects released for biological control, and island mammals, all of which had higher establishment success than predicted by this generalization (221).

Surveys of mosquito fauna arriving in the continental United States by international aircraft (50, 84) and ship (34) provide estimates of the number of species arriving via these transport mechanisms. In international aircraft disinfected between 1948–1960, 18 nonindigenous mosquito species were intercepted at airports in the continental United States (84) and 4 more species in tires on container ships

from Japan (34). For Hawaii, the number of mosquito species detected on aircraft was 33 (50, 84). Nonindigenous mosquito species in the continental United States include not only the five twentieth-century introductions of container occupants (Table 1), but also *Ae. aegypti*, *Cx. pipiens*, and *Cx. quinquefasciatus*, the latter two members of the *Cx. pipiens* Complex believed to have arrived by ships from the Old World (166). [DNA microsatellite genotype similarities support a West African origin of North American *Cx. quinquefasciatus* (D. Fonseca, personal communication).] The percentages of biting mosquitoes that became established are much higher for the continental United States ( $8/22 = 36.4\%$ ), but within the 5–20% confidence limits for Hawaii ( $5/33 = 15.2\%$ ), based on predictions by the Tens Rule. Mosquito interceptions from international aircraft and ships arriving in Australia have detected 16 nonindigenous mosquito species (173, 211; R.C. Russell, personal communication), yielding a 25% ( $4/16$ ) establishment success. According to these calculations, the Tens Rule generally underestimates establishment success of mosquito arrivals. However, given that the North American mosquito identifications from aircraft were done more than 40 years ago, when international travel was less frequent and only ships at a few American and Australian ports were inspected, the denominators of these calculations undoubtedly underestimate the actual number of nonindigenous species of arriving mosquitoes. *Culex quinquefasciatus* is the only one of many nonindigenous species detected on aircraft arriving in Hawaii that became established (although it reached Hawaii via ships). By contrast, two of the four species detected on ships by Craven et al. (34), *Ae. albopictus* and *Ae. togoi*, are now established in the United States.

The second Tens Rule transition, from established to pest status, where pest is defined as “with a negative economic effect” (219, 221), is more difficult to apply to invasive disease vectors. A more apt negative transition would be involvement in the transmission of pathogens to humans. Among the 40 established invaders counted for Table 2, only *Ae. aegypti* as a vector of dengue in northern Australia and *Ae. albopictus* as a probable vector of La Crosse encephalitis virus in the United States (61) are currently involved in human disease transmission. Thus, for the six localities listed in Table 2,  $2/40$  (5.0%) of the invasive species have become disease vectors in their new environs, which is within the confidence limits of the Tens Rule.

## DETERMINANTS OF INVASION SUCCESS

Williamson (220) has pointed out that the best correlates of invasion success, propagule pressure and previous success, are not truly biological. Population characteristics, such as abundance, range, or intrinsic rate of increase, or individual traits, such as climate matching, niche availability, or taxonomic isolation, are often moderate or poor correlates of invasion success (220). Certainly, propagule pressure and previous success appear to have favored the invasions of the three

most successful mosquito dispersers, *Ae. aegypti*, the *Cx. pipiens* Complex, and *Ae. albopictus*, which have become nearly cosmopolitan or cosmopolitan through successive waves of human-aided dispersal (21).

Regarding propagule pressure, it is noteworthy that most successful mosquito invaders have arrived by ship. Among the 40 instances of culicid invaders recorded in Table 2, only *Cx. gelidus* in Brisbane (128), *Ae. vexans* in Hawaii (90) and a few species of mosquitoes in Guam (208) appear to have arrived on aircraft. The comparatively poor invasion success of aircraft arrivals may be due to the strong relationship between release size and the probability of population establishment (67, 68). Mosquito arrivals on aircraft are typically adults consisting of only a few individuals of any given species (50, 84). However, ships, especially modern container vessels (156, 157), can carry a large number of propagules, especially of the immature stages, of mosquitoes. The transport of desiccation-resistant *Aedes* eggs, especially in tires, may account for the establishment of such container-frequenting species as *Ae. togoi* in the Pacific Northwest (11) and Malaysia (150), *Ae. bahamensis* in south Florida (145), and *Ae. atropalpus* in Italy (163), as well as *Ae. albopictus* worldwide and *Ae. japonicus* in the United States. If Guam is omitted, mosquitoes of the genus *Aedes* account for 65.2% (15/23) of the successful mosquito invaders tallied for Table 2.

The dominance of a few species among the successful mosquito invaders suggests that previous success may be a potentially good predictor of vector invasiveness. The three most widely distributed mosquito species, cited above, have achieved this status through human-aided "jump" dispersals (186) followed by regional spread. The recent intercontinental dispersal of two additional tire-inhabiting species, *Ae. japonicus* and *Ae. atropalpus* (149, 163), may represent another wave of "repeat" invaders.

Elton (49) postulated that simple biological communities are more vulnerable to invasions, but Levine & D'Antonio (100) reviewed both models and observational and experimental studies and found no clear relationship between community diversity and invasibility. Elton (49) also presumed that islands are more susceptible to invasions than mainland communities, but Simberloff (185, 186) suggested that this difference is more apparent than real. Indeed, inspection of mosquito invasions from the nonrandom selection of four islands and two continental nations would seem to indicate no obvious relationships among these factors (Table 2). For example, the smaller, less diverse island nation of New Zealand has as many species of mosquito invaders as its much larger and more biologically diverse neighbor Australia, and smaller Guam has many more invasive mosquito species than Hawaii. Although the reasons for this variability among islands are not known, nonbiological factors, such as the frequency of noninspected arrivals of air and sea transport, may be important determinants of invasion success on these islands.

For phytophagous insects that live on trees and shrubs, 75% of the 400 invasive species in North America are of European origin (117). Although this high rate may be attributable partly to early trade routes, Niemelä & Mattson (140) have suggested that European phytophagous insects may be better competitors than

their North American counterparts. However, among eight species of invasive mosquitoes in the continental United States only *Cx. pipiens* s.s. is probably of European origin (166), suggesting no competitive advantage for European culicids in North America. Three species of twentieth century mosquito invaders of the United States are of Oriental origin, which corresponds to the predominant direction of tire exports (156).

## INVASION BIOLOGY AND VECTOR CONTROL

Studies of invasion processes have broad applicability to vector control beyond the interception of unwanted arrivals or suppression of recent infestations. For example, the release, establishment, and spread of a pathogen or parasite for the biological control of a vector (203) follows dynamics comparable to an unintended invasion (67, 68). Similarly, genetic engineering approaches to vector control by population replacement (73) require the release of genetically altered organisms that will behave like invading propagules in the native vector habitat. Reinvasions of vectors after eradication schemes, such as that of the Onchocerciasis Control Program in West Africa (207) or the partial eradication of *Ae. aegypti* from the Americas (190), obey the population dynamics of arrival, establishment, and spread common to new invaders.

The unanticipated competitive displacement of *Ae. aegypti* in the southeastern United States by invasive *Ae. albopictus* (80, 91, 143) corroborated a principle in vector control tested many years earlier in an unsuccessful field experiment. Based on its superior competitive ability in laboratory comparisons (e.g., 71, 108), Rosen et al. (165) released large numbers of *Ae. albopictus* on a coral atoll, but this nonindigenous species failed to displace the native filarial vector *Aedes polynesiensis* and within 1–4 years disappeared from the island. Just as laboratory experiments were misleading about the competitive outcome of recent *Ae. albopictus*–*Ae. aegypti* encounters in the southern United States (91), laboratory simulations failed to predict the results of the *Ae. albopictus*–*Ae. polynesiensis* interaction on the atoll. Perhaps lessons learned from unintended invasions will instruct future considerations of experimental competitive displacement for vector control.

## FUTURE DIRECTIONS AND NEEDS

Identifying future invaders is critically important because eradication of an established invader, as accomplished over 60 years ago for *An. gambiae* in Brazil (191), is rarely possible (110). Ecological shifts that promote the exploitation of habitats associated with human activities have accompanied many previous successful vector invasions and may provide clues to future threats. However, invasion biology is far from being a predictive science (219, 220).

In the wake of the diaspora of *Ae. albopictus* (33) that is still underway, it is hard to imagine what might be next in the worldwide reshuffling and homogenization of vector faunal distributions promoted by human-aided transport. In addition to transport systems, global climate changes could alter the boundaries of vector limits and distributions (115) and influence the invasion potential of species and habitats (105).

Because the application of invasion biology to vectors is new, this review is largely an accounting of past and recent events, some with important epidemiological consequences. Improved surveillance, such as the close scrutiny of the spread of *Ae. albopictus* in the United States and Italy, has provided more accurate data than previously available on the arrival and establishment of some invaders. However, on a global scale, most vector invasions probably go unnoticed because of a lack of surveillance [the presence of *Ae. albopictus* in Nigeria was recognized only because of a visit by a CDC surveillance team following a yellow fever epidemic (175)], and comprehensive data on the components of invasions by vectors are available for only a few regions. Generalizations, explanations, and predictions are hampered by a lack of detection and/or follow-up of invading vectors in most areas of the world and the absence of a universal reporting system.

Sensitive molecular genetic markers have great potential for tracing the origins and frequencies of vector introductions but are only just beginning to be used (e.g., 12a, 53, 54). Ideally, they are best suited if deployed at the earliest stages of an invasion. In order to characterize invasions beyond descriptive stages, experimentation, especially field manipulations (e.g., 91), will be increasingly important to explain the biological outcomes, such as competitive displacement, of invasions. As more quantitative ecological data become available to explain invasion patterns, such as that of *Ae. albopictus* in the United States, Brazil, and Italy (Figure 2), generalizations about invulnerable communities and species may be realized (205). These generalizations could be potentially important for guiding future initiatives in vector control, such as by the release of transgenic mosquitoes, whose population dynamics may mimic invasive species.

The impact of invasive vectors on human ecosystems is measured most appropriately in health consequences and hence is quite different from the economics of nonvector invaders (147). When a recently established vector promptly becomes the primary transmitter in an epidemic, as for malaria in Brazil in the 1930s and in Peru in the 1990s, the health impacts are obvious. On the other hand, as noted by Elton (49) for the gypsy moth, the negative consequences of an invasion may not be felt for a long period after establishment. The insinuation of a new vector into a multicomponent zoonosis, such as for *Ae. albopictus* with La Crosse virus (61), is liable to occur more gradually after invasion and requires careful monitoring. In addition, viruses may evolve within new vectors, potentially changing their pathogenicity and transmissibility (28). Whereas the physiological and molecular events of new vector-pathogen combinations may be examined experimentally in the lab, possible epidemiological consequences warrant a modeling approach, as has been applied to some noninsect-borne infectious diseases (182).

## ACKNOWLEDGMENTS

For personal communications and access to prepublications I am grateful to T. Andreadis, C. Apperson, G. Browne, D. Fonseca, K. Gage, K. Gottfried, L. Munstermann, R. Lourenço-de-Oliveira, G. O'Meara, R. Romi, and R. Russell. For comments on a draft of this manuscript I thank S. Juliano, C. Moore, G. O'Meara, and W. Tabachnick. Work on this review was supported, in part, by NIH grant AI-44793. This is University of Florida Agricultural Experiment Station Publication No. R-08084.

Visit the Annual Reviews home page at [www.AnnualReviews.org](http://www.AnnualReviews.org)

## LITERATURE CITED

- Adhami J, Reiter P. 1998. Introduction and establishment of *Aedes (Stegomyia) albopictus* Skuse (Diptera: Culicidae) in Albania. *J. Am. Mosq. Control Assoc.* 14:340-43
- Allaby M, ed. 1998. *Oxford Dictionary of Ecology*. New York: Oxford Univ. Press. 440 pp. 2nd ed.
- Andreadis TG. 1988. A survey of mosquitoes in used tire stockpiles in Connecticut. *J. Am. Mosq. Control Assoc.* 4:256-60
- Andreadis TG, Anderson JF, Munstermann LE, Wolfe RJ, Florin DA. 2001. Discovery, distribution, and abundance of the newly introduced mosquito *Ochlerotatus japonicus* (Diptera: Culicidae) in Connecticut, USA. *J. Med. Entomol.* 38(6): In press
- Arambarú Guarda J, Ramal Ayasag C, Witzig R. 1999. Malaria reemergence in the Peruvian Amazon region. *Emerg. Infect. Dis.* 5:209-15
- Azevedo J Fraga de, Tendeiro J, Franco LT de Almeida, Murao M da C, et al. 1958. Les glossines de nouveau a l'Ile de Prince. *Comm. Tech. Coop. Afr. South Sahara, 7th, London, Publ. No. 41*, pp. 321-30
- Barrera R. 1996. Competition and resistance to starvation in larvae of container-inhabiting *Aedes* mosquitoes. *Ecol. Entomol.* 21:117-27
- Barrett TV, Hoff R, Mott KE, Guedes F, Sherlock IA. 1979. An outbreak of acute Chagas's disease in the São Francisco valley region of Bahia, Brazil: triatomine vectors and animal reservoirs of *Trypanosoma cruzi*. *Trans. R. Soc. Trop. Med. Hyg.* 73:703-9
- Baumgartner DL. 1988. Suburban accumulations of discarded tires in north-eastern Illinois and their associated mosquitoes. *J. Am. Mosq. Control Assoc.* 4:500-8
- Belkin JN. 1968. Mosquito studies (Diptera: Culicidae). VII. The Culicidae of New Zealand. *Contrib. Am. Entomol. Inst.* 3(1):1-182
- Belton P, Belton OC. 1990. *Aedes togoi* comes aboard. *J. Am. Mosq. Control Assoc.* 6:328-29
- Berry WJ, Craig GB. 1984. Bionomics of *Aedes atropalpus* breeding in scrap tires in northern Indiana. *Mosq. News* 44:476-84
- 12a. Birungi J, Munstermann LE. 2002. Genetic structure of *Aedes albopictus* (Diptera: Culicidae) populations based on mitochondrial ND5 sequences: evidence for an independent invasion into Brazil and the United States. *Ann. Entomol. Soc. Am.* In press
13. Black WC, Ferrari JA, Rai KS, Sprenger D. 1988. Breeding structure of a colonizing species: *Aedes albopictus* (Skuse) in the United States. *Heredity* 60:173-81
14. Black WC, Hawley WA, Rai KS, Craig



- GB. 1988. Breeding structure of a colonizing species: *Aedes albopictus* (Skuse) in peninsular Malaysia and Borneo. *Heredity* 61:439–46
15. Black WC, Rai KS, Turco BJ, Arroyo DC. 1989. Laboratory study of competition between United States strains of *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae). *J. Med. Entomol.* 26: 260–71
  16. Blazquez J. 1987. Paludismo de aeropuerto en España. *Med. Clin. (Barcelona)* 88:51
  17. Bohart RM. 1956. Diptera: Culicidae. In *Insects of Micronesia*, 12(1). Honolulu, HI: Bishop Mus. 85 pp.
  18. Boorman J. 1993. Biting midges (Ceratopogonidae). In *Medical Insects and Arachnids*, ed RP Lane, RW Crosskey, pp. 288–309. London: Chapman & Hall
  19. Broche RG, Borja EM. 1999. *Aedes albopictus* in Cuba. *J. Am. Mosq. Control Assoc.* 15:569–70
  20. Bryan WA. 1915. *Natural History of Hawaii*. Honolulu, HI: Hawaiian Gazette Co. 596 pp.
  21. Calder L, Laird M. 1994. Mosquito travelers, arbovirus vectors and the used tire trade. *Trav. Med. Int.* 12:3–12
  22. Calderón G, Curaca A, Llancari J, Napán M, Sipán Y. 1974. Distribución geográfica de los vectores de malaria en el Perú. *Rev. Per. Med. Trop.* 2:88–91
  23. Carey JR, Moyle P, Moyle R, Vermeij G, eds. 1996. Invasion biology. *Biol. Conserv.* 78:1–214
  24. Carlton JT, ed. 1999. *Biological Invasions*. Vol. 1. Dordrecht, The Netherlands: Kluwer
  25. Causey OR, Deane LM, Deane MP. 1943. Ecology of *Anopheles gambiae* in Brazil. *Am. J. Trop. Med. Hyg.* 23:73–94
  26. Causey OR, Penido HM, Deane LM. 1943. Observations on malaria in the presence and absence of *Anopheles gambiae* in an experimental area in (Cumbe) Ceará, Brazil. *Am. J. Trop. Med. Hyg.* 23:59–71
  27. Centers for Disease Control. 2000. Update: West Nile virus activity—eastern United States, 2000. *MMWR* 49:1044–47
  28. Cheng L, Rodas JD, Schultz KT, Christensen BM, Yuill TM, et al. 1999. Potential for evolution of California serogroup bunyaviruses by genome reassortment in *Aedes albopictus*. *Am. J. Trop. Med. Hyg.* 60:430–38
  29. Christophers RC. 1960. *Aedes aegypti. The Yellow Fever Mosquito: Its Life History, Bionomics, and Structure*. Cambridge: Cambridge Univ. Press. 739 pp.
  30. Cloudsley-Thompson JL. 1976. *Insects and History*. New York: St. Martin's. 242 pp.
  31. Covell CJ, Brownell AJ. 1979. *Aedes atropalpus* in abandoned tires in Jefferson County, Kentucky. *Mosq. News* 39:142
  32. Cox GW. 1999. *Alien Species in North America and Hawaii. Impacts on Natural Ecosystems*. Washington, DC: Island. 387 pp.
  33. Craig GB. 1993. The diaspora of the Asian Tiger Mosquito. See Ref. 118, pp. 101–20
  34. Craven RB, Eliason DA, Francy DB, Reiter P, Campos EG, et al. 1988. Importation of *Aedes albopictus* and other exotic mosquito species into the United States in used tires from Asia. *J. Am. Mosq. Control Assoc.* 4:138–42
  35. Crawley MJ, Harvey PH, Purvis A. 1996. Comparative ecology of the native and alien florae of the British isles. *Phil. Trans. R. Soc. London Ser. B* 351:1251–59
  36. Curtis CF, White GB. 1984. *Plasmodium falciparum* transmission in England: entomological and epidemiological data relative to cases in 1983. *J. Trop. Med. Hyg.* 87:101–14
  37. Daehler CC. 2001. Two ways to be an invader, but one is more suitable for ecology. *Bull. Ecol. Soc. Am.* 81:101–2
  38. Darsie RF, Ward RA. 2000. Summary of new distribution records for mosquito species in the United States and Canada for the period 1981–99. *J. Am. Mosq. Control Assoc.* 16:1–4

- 38a. Da Silveira AC. 1998. Dengue: aspectos epidemiológicas e de control. *Rev. Soc. Bras. Med. Trop.* 31:5-14
39. Davis MA, Thompson K. 2000. Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bull. Ecol. Soc. Am.* 81:226-30
40. Deane LM. 1988. Malaria studies and control in Brazil. *Am. J. Trop. Med. Hyg.* 38:223-30
41. DeTavel F. 1967. Measures to be taken to prevent the transmission of *Aedes aegypti* by sea and air. *Bull. WHO* 36:639-44
42. DiCasteri F, Hansen AJ, Debussche M, eds. 1990. *Biological Invasions in Europe and the Mediterranean Basin*. Dordrecht, The Netherlands: Kluwer. 463 pp.
43. Dine DLV. 1904. Mosquitoes in Hawaii. *Bull. Hawaii Agric. Exp. Stn.* 6. 30 pp.
44. Drake JA, Mooney HA, DiCasteri F, Groves RH, Kruger FJ, et al., eds. 1989. *Biological Invasions, A Global Perspective*. Chichester, UK: Wiley. 525 pp.
45. Dujardin JP, Muñoz M, Chavez T, Ponce C, Moreno J, et al. 1998. The origin of *Rhodnius prolixus* in Central America. *Med. Vet. Entomol.* 12:113-15
46. Duplax N. 1988. Fleas. The lethal leapers. *Nat. Geogr.* 173:672-94
47. Eads RB. 1972. Recovery of *Aedes albopictus* from used tires shipped to United States ports. *Mosq. News* 32:113-14
48. Edgerly JS, Willey MS, Livdahl TP. 1993. The community ecology of *Aedes* egg hatching: implications for a mosquito invasion. *Ecol. Entomol.* 18:123-28
49. Elton CS. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen. 181 pp.
50. Evans BR, Joyce CR, Porter JE. 1963. Mosquitoes and other arthropods found in baggage compartments of international aircraft. *Mosq. News* 23:9-22
51. Fernandez RF, Carbajal J, Quintana J, Chauca H, Watts DM. 1996. Presencia del *A. (N.) darlingi* (Diptera: Culicidae) en alrededores de la ciudad de Iquitos Loreto-Peru. *Bol. Soc. Per. Enferm. Infecc. Trop.* 5:10-12
52. Focks DA, Sackett SR. 1985. Some factors affecting interactions of *Toxorhynchites amboinensis* with *Aedes* and *Culex* in an urban environment. In *Ecology of Mosquitoes. Proceedings of a Workshop*, ed. LP Lounibos, JR Rey, JH Frank, pp. 55-64. Vero Beach, FL: Fla. Med. Entomol. Lab. 579 pp.
53. Fonseca DM, Campbell S, Crans WJ, Mogi M, Miyagi I, et al. 2001. *Aedes (Finlaya) japonicus* (Diptera: Culicidae), a newly recognized mosquito in the United States: analyses of genetic variation in the United States and putative source populations. *J. Med. Entomol.* 38:135-46
54. Fonseca DM, LaPointe DA, Fleischer RC. 2000. Bottlenecks and multiple introductions: population genetics of the vector of avian malaria in Hawaii. *Molec. Ecol.* 9:1803-14
55. Forattini OP. 1986. Identificação de *Aedes (Stegomyia) albopictus* (Skuse) no Brasil. *Rev. Saúde Publ.* 20:244-45
56. Francly DB, Karabatsos N, Wesson DM, Moore CG, Lazuick JS, et al. 1990. A new arbovirus from *Aedes albopictus*, an Asian mosquito established in the United States. *Science* 250:1738-40
57. Frank JH, McCoy ED, Hall GH, O'Meara GF, Tschinkel WR. 1997. Immigration and introduction of insects. See Ref. 187, pp. 75-99
58. Freedman FJH. 1969. Outbreaks of the blackfly *Simulium arcticum* Malloch in Alberta. *Quaest. Entomol.* 5:341-72
59. Gamboa CJ. 1962. Dispersión de *Rhodnius prolixus* en Venezuela. *Bol. Dir. Malar. San. Amb.* 3:262-72
60. Garms R, Walsh JF. 1987. The migration and dispersal of black flies: *Simulium damnosum* s.l., the main vector of human onchocerciasis. In *Black Flies: Ecology, Population Management, and Annotated World List*, ed. KC Kim, RW Merritt, pp.

- 201–14. University Park, PA: Pennsylvania Univ. Press
61. Gerhardt RR, Gottfried KL, Apperson CS, Davis BS, Erwin PC, et al. 2001. First isolation of La Crosse virus from naturally infected *Aedes albopictus*. *Emerg. Infect. Dis.* 37(5): In press
  62. Gillies MT, Coetzee M. 1987. *A Supplement to the Anophelinae of Africa South of the Sahara*. Johannesburg: Publ. South Afr. Inst. Med. Res. No. 55. 143 pp.
  63. Goldsmit JM. 1984. The introduction of vectors and disease into Australia: an historical perspective and present-day threat. See Ref. 97, pp. 143–62
  64. Gomes AC, Bitencourt MD, Natal D, Pinto PLS, Mucci LF, et al. 1999. *Aedes albopictus* em area rural do Brasil e implicações na transmissão de febre amarela silvestre. *Rev. Saúde Publ.* 33:95–97
  65. Gray AJ, Crawley MJ, Edwards PJ, eds. 1987. *Colonization, Succession and Stability*. 26th Symp. Br. Ecol. Soc. Oxford, UK: Blackwell Scientific. 485 pp.
  66. Green RE. 1997. The influence of numbers released on the outcomes of attempts to introduce exotic bird species to New Zealand. *J. Anim. Ecol.* 66:25–35
  67. Grevstad FS. 1999. Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biol. Invas.* 1:313–23
  68. Grevstad FS. 1999. Factors influencing the chance of population establishment: implications for release strategies in bio-control. *Ecol. Appl.* 9:1439–47
  69. Griffiths THD, Griffiths JJ. 1931. Mosquitoes transported by airplanes: staining methods used in determining their importation. *Public Health Rep.* 46(47): 2775–82
  70. Groves RH, DiCastrì F, eds. 1991. *Biogeography of Mediterranean Invasions*. Cambridge: Cambridge Univ. Press. 485 pp.
  71. Gubler DJ. 1970. Competitive displacement of *Aedes (Stegomyia) polynesiensis* Marks by *Aedes (Stegomyia) albopictus* Skuse in laboratory populations. *J. Med. Entomol.* 7:229–35
  72. Gubler DJ, Clark GC. 1995. Dengue/dengue hemorrhagic fever: the emergence of a global health problem. *Emerg. Infect. Dis.* 1:55–57
  73. Gwadz RW. 1994. Genetic approaches to malaria control: how long the road? *Am. J. Trop. Med. Hyg.* 50(Suppl.):116–25
  74. Harrison BA, Mitchell CJ, Apperson CS, Smith GC, Karabatsos N, et al. 1995. Isolation of Potosi virus from *Aedes albopictus* in North Carolina. *J. Am. Mosq. Control Assoc.* 11:225–29
  75. Harrison G. 1978. *Mosquitoes, Malaria and Man: A History of the Hostilities Since 1880*. London: John Murray. 314 pp.
  76. Hawley WA. 1988. The biology of *Aedes albopictus*. *J. Am. Mosq. Control Assoc.* 4(Suppl.):1–40
  77. Hawley WA, Reiter P, Copeland RS, Pumpuni CB, Craig GB. 1987. *Aedes albopictus* in North America: probable introduction in used tires from Northern Asia. *Science* 236:1114–16
  78. Hearden M, Skelly C, Weinstein P. 1999. Improving the surveillance of mosquitoes with disease-vector potential in New Zealand. *NZ Public Health Rep.* 6:25–28
  79. Ho BG, Ewert A, Chew LM. 1989. Interspecific competition among *Aedes aegypti*, *Ae. albopictus* and *Ae. triseriatus* (Diptera: Culicidae): larval development in mixed cultures. *J. Med. Entomol.* 26:615–23
  80. Hobbs JH, Hughes EA, Eichold BH. 1991. Replacement of *Aedes aegypti* by *Aedes albopictus* in Mobile, Alabama. *J. Am. Mosq. Control Assoc.* 7:488–89
  81. Holvoet G, Michielsen P, Vandepitte J. 1983. Autochthonous falciparum malaria in Belgium. *Ann. Soc. Belg. Med. Trop.* 63:111–17
  82. Hopla CE. 1980. A study of the host associations and zoogeography of *Pulex*. In *Fleas. Proc. Intern. Conf. Fleas,*

- Ashton Wold/Peterborough/UK, ed. R Traub, H Starcke, pp. 185–207. Rotterdam, The Netherlands: AA Balkema. 420 pp.
83. Hsaio T, Bohart RM. 1946. The mosquitoes of Japan and their medical importance. *US Dep. Navy Navmed.* 1095:1–44
  84. Hughes JN. 1961. Mosquito interceptions and related problems in aerial traffic arriving in the United States. *Mosq. News* 21:93–100
  85. Ibañez-Bernal S, Briseño B, Mutebi J-P, Argot E, Rodriguez G, et al. 1997. First record in America of *Aedes albopictus* naturally infected with dengue virus during the 1995 outbreak at Reynosa, Mexico. *Med. Vet. Entomol.* 11:305–9
  86. Ibañez-Bernal S, Martínez-Campos C. 1994. *Aedes albopictus* in Mexico. *J. Am. Mosq. Control Assoc.* 10:231–32
  87. Janousek TE, Kramer WL. 1999. Seasonal incidence and geographical variation of Nebraska mosquitoes, 1994–95. *J. Am. Mosq. Control Assoc.* 15:253–62
  88. Joenje W, Bakker K, Vlijm L, eds. 1987. The ecology of biological invasions. *Proc. Kon. Neder. Akad. Wet.* 90:1–80
  89. Joyce CR. 1961. Potentialities for accidental establishment of exotic mosquitoes in Hawaii. *Proc. Hawaii Entomol. Soc.* 17:403–13
  90. Joyce CR, Nakagawa PY. 1963. *Aedes vexans nocturnus* (Theobald) in Hawaii. *Proc. Hawaii Entomol. Soc.* 1:64–67
  91. Juliano SA. 1998. Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? *Ecology* 79:255–68
  92. Kambhampati S, Black WC, Rai KS. 1991. Geographic origin of US and Brazilian *Aedes albopictus* inferred from allozyme analysis. *Heredity* 67:85–94
  93. Karieva P, ed. 1996. Advances in invasion ecology. *Ecology* 77:1651–97
  94. Knight KL. 1967. Distribution of *Aedes sollicitans* (Walker) and *Aedes taeniorhynchus* (Wiedemann) within the United States (Diptera: Culicidae). *J. Ga. Entomol. Soc.* 2:9–12
  95. Kornberg H, Williamson MW, eds. 1987. Quantitative aspects of the ecology of biological invasions. *Phil. Trans. R. Soc. London Ser. B* 314:501–742
  96. Laird M. 1948. Reactions of mosquitoes to the aircraft environment. *Trans. R. Soc. NZ* 77:93–114
  97. Laird M, ed. 1984. *Commerce and the Spread of Pests and Disease Vectors*. New York: Praeger. 354 pp.
  98. Laird M. 1984. Overview and perspectives. See Ref. 97, pp 291–325
  99. Laird M, Calder L, Thornton RC, Syme R, Holder PW, et al. 1994. Japanese *Aedes albopictus* among four mosquito species reaching New Zealand in used tires. *J. Am. Mosq. Control Assoc.* 10:14–23
  100. Levine JM, D'Antonio CM. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26
  101. Lewis RE. 1972. Notes on the geographical distribution and host preferences in the order Siphonaptera. *J. Med. Entomol.* 9:511–20
  102. Lewis RE. 1993. Fleas (Siphonaptera). In *Medical Insects and Arachnids*, ed. RP Lane, RW Crosskey, pp. 529–75. London: Chapman & Hall. 723 pp.
  103. Link VB. 1954. A history of plague in the United States of America. *Public Health Monogr. No. 26*. Washington, DC: GPO. 120 pp.
  104. Livdahl T, Willey MS. 1991. Prospects for an invasion: competition between *Aedes albopictus* and native *Aedes triseriatus*. *Science* 253:189–91
  105. Lodge DM. 1993. Biological invasions: lessons for ecology. *Trends Ecol. Evol.* 8:133–37
  106. Lounibos LP, Conn JE. 2000. Malaria vector heterogeneity in South America. *Am. Entomol.* 46:238–49
  107. Lounibos LP, O'Meara GF, Escher RL, Nishimura N, Cutwa M, et al. 2002. Testing predictions of displacement of native *Aedes* by the invasive Asian Tiger

- Mosquito *Aedes albopictus* in Florida, USA. *Biol. Invas.* In press
108. Lowrie RC. 1973. Displacement of *Aedes* (*S.*) *polynesiensis* Marks by *A.* (*S.*) *albopictus* Skuse through competition in the larval stage under laboratory conditions. *J. Med. Entomol.* 10:131–36
  109. Macdonald IAW, Kruger FJ, Ferrar AA, eds. 1986. *The Ecology and Management of Biological Invasions in Southern Africa*. Cape Town: Oxford Univ. Press
  110. Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, et al. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10:689–710
  111. Manguin S, Roberts DR, Andre RG, Rejmankova E, Hakre S. 1996. Characterization of *Anopheles darlingi* (Diptera: Culicidae) larval habitats in Belize, Central America. *J. Med. Entomol.* 33:205–11
  112. Marchant P, Eling G, Van Gemert G-J, Leake CJ, Curtis CF. 1998. Could British mosquitoes transmit falciparum malaria? *Parasitol. Today* 14:344–45
  113. Marks EN. 1972. Mosquitoes (Culicidae) in the changing Australian environment. *Qd. Nat.* 20:101–16
  114. Marques CCA, Marques GRA, Degallier N. 1998. Is *Aedes albopictus* only a pest mosquito or also a vector of arboviruses in Brazil? In *An Overview of Arbovirology in Brazil and Neighbouring Countries*, ed. APA Travassos da Rosa, PFC Vasconcelos, JFS Travassos da Rosa, pp. 248–60. Belem, Brazil: Instit. Evandro Chagas. 296 pp.
  115. Martens P. 1998. *Health and Climate Change: Modelling the Impacts of Global Warming and Ozone Depletion*. London: Earthscan
  116. Mattingly PF. 1958. The sub-genus *Stegomyia* (Diptera: Culicidae) in the Ethiopian Region. II. Distribution of species confined to the East and South African sub-region. *Bull. Br. Mus. (Nat. Hist.) Entomol.* 3:1–65
  117. Mattson WJ, Niemalä P, Millers I, Inguanzo Y. 1994. Immigrant phytophagous insects on woody plants in the United States and Canada: an annotated list. *Gen. Tech. Rep. NC-169*. St. Paul, MN: USDA
  118. McKnight BN, ed. 1993. *Biological Pollution: The Control and Impact of Invasive Exotic Species*. Indianapolis, IN: Indiana Acad. Sci. 261 pp.
  119. McNeil WH. 1976. *Plagues and Peoples*. Garden City, NY: Anchor/Doubleday. 369 pp.
  120. Mekuria Y, Hyatt MG. 1995. *Aedes albopictus* in South Carolina. *J. Am. Mosq. Control Assoc.* 11:468–70
  121. Mitchell CJ. 1991. Vector competence of North and South American strains of *Aedes albopictus* for certain arboviruses. *J. Am. Mosq. Control Assoc.* 7:446–51
  122. Mitchell CJ. 1995. Geographic spread of *Aedes albopictus* and potential for involvement in arbovirus cycles in the Mediterranean Basin. *J. Vect. Ecol.* 20:44–58
  123. Mitchell CJ, Niebylski ML, Karabatsos N, Martin D, Mutebi J-P, et al. 1992. Isolation of eastern equine encephalitis from *Aedes albopictus* in Florida. *Science* 257:526–27
  124. Mooney HA, Drake JA, eds. 1986. *Ecology of Biological Invasions of North America and Hawaii*, Ecological Studies Vol. 58. New York: Springer-Verlag. 321 pp.
  125. Mooney HA, Hobbs RJ, eds. 2000. *Invasive Species in a Changing World*. Washington, DC: Island. 457 pp.
  126. Moore CG. 1999. *Aedes albopictus* in the United States: current status and prospects for further spread. *J. Am. Mosq. Control Assoc.* 15:221–27
  127. Moore CG, Mitchell CJ. 1997. *Aedes albopictus* in the United States: ten-year presence and public health implications. *Emerg. Infect. Dis.* 3:329–34
  128. Muller M. 1999. Detection of *Culex gelidus* in Brisbane. *Bull. Mosq. Control Assoc. Aust.* 11:13–16

129. Munstermann LE, Andreadis TG. 1999. *Aedes japonicus* in Connecticut. *Vector Ecol. News.* 30:7-8
130. Munstermann LE, Wesson DM. 1990. First record of *Ascogregarina taiwanensis* (Apicomplexa: Leucudinidae) in North American *Aedes albopictus*. *J. Am. Mosq. Control Assoc.* 6:235-43
131. Murray MD, Kirkland PD. 1995. Blue-tongue and Douglas virus activity in New South Wales in 1989: further evidence for long-distance dispersal of the biting midge *Culicoides brevitarsis*. *Aust. Vet. J.* 72:56-57
132. Nakagawa PY, Hirst JM. 1959. Current efforts in mosquito control in Hawaii. *Mosq. News* 19:64-67
133. Nasci RS, Hare CG, Willis FS. 1989. Interspecific mating between Louisiana strains of *Aedes albopictus* and *Aedes aegypti* in the field and the laboratory. *J. Am. Mosq. Control Assoc.* 5:416-21
134. Nash TAM. 1969. *Africa's Bane. The Tsetse Fly*. London: Collins. 224 pp.
135. Natal D, Urbinatti PR, Taípe-Lagos C, Ceret W, Diederichsen A, et al. 1997. Encontro de *Aedes (Stegomyia) albopictus* em Bromeliaceae na periferia de São Paulo, SP, Brasil. *Rev. Saúde Publ.* 31:517-18
136. Nawrocki SJ, Hawley WA. 1987. Estimation of the northern limits of distribution of *Aedes albopictus* in North America. *J. Am. Mosq. Control Assoc.* 3:314-17
137. Need JT, Rogers EJ, Phillips IA, Falcón R, Fernandez R, et al. 1993. Mosquitoes (Diptera: Culicidae) captured in the Iquitos area of Peru. *J. Med. Entomol.* 30:634-38
138. Neiva A. 1915. Contribuição para o conhecimento dos hemipteros hematofagos da America Central. *Braz. Med.* 29:1-3
139. New Zealand Ministry of Health. 1999. Update—exotic mosquitoes in Hawke's Bay. <http://www.moh.govt.nz/moh.nsf/>
140. Niemelä P, Mattson WJ. 1996. Invasion of North American forests by European phytophagous insects. *Bioscience* 46:741-53
141. Ogata K, Lopez Samayoa A. 1996. Discovery of *Aedes albopictus* in Guatemala. *J. Am. Mosq. Control Assoc.* 12:503-6
142. O'Meara GF, Evans LF. 1997. Discovery of a bromeliad-inhabiting *Culex (Micraeodes)* sp. in south Florida. *J. Am. Mosq. Control Assoc.* 13:208-10
143. O'Meara GF, Evans LF, Gettman AD, Cuda JP. 1995. Spread of *Aedes albopictus* and decline of *Ae. aegypti* (Diptera: Culicidae) in Florida. *J. Med. Entomol.* 32:554-62
144. O'Meara GF, Gettman AD, Evans LF, Curtis GA. 1993. The spread of *Aedes albopictus* in Florida. *Am. Entomol.* 39:163-72
145. O'Meara GF, Larson VL, Mook DH, Latham MD. 1989. *Aedes bahamensis*: its invasion of south Florida and association with *Aedes aegypti*. *J. Am. Mosq. Control Assoc.* 5:1-5
- 145a. O'Meara GF, Lounibos LP, Cutwa MM, Nishimura N, et al. 2002. Persistence of *Aedes aegypti* in south Florida following the *Aedes albopictus* invasion. *J. Med. Entomol.* In press
146. Pafume BA, Campos EG, Francy DB, Peyton EL, Davis AN, et al. 1988. Discovery of *Aedes (Howardina) bahamensis* in the United States. *J. Am. Mosq. Control Assoc.* 4:380
147. Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invas.* 1:3-19
148. Peña C. 1993. First report of *Aedes (Stegomyia) albopictus* (Skuse) from the Dominican Republic. *Vect. Ecol. News.* 24(4):4-5
149. Peyton EL, Campbell SR, Candeletti TM, Romanowski M, Crans WJ. 1999. *Aedes (Finlaya) japonicus japonicus* (Theobald), a new introduction into the

- United States. *J. Am. Mosq. Control Assoc.* 15:238-41
150. Pillai JS, Ramalingam S. 1984. Recent introductions of some medically important Diptera in the Northwest, Central, and South Pacific (including New Zealand). See Ref. 97, pp. 81-101
  151. Pimentel D, Lach L, Zuniga R, Morrison D. 2000. Environmental and economic costs of non-indigenous species in the United States. *Bioscience* 50:53-65
  152. Pinho AP, Goncalves TCM, Mangia RH, Russell NSN, Jansen AM. 1998. The occurrence of *Rhodnius prolixus* Stal, 1859, naturally infected by *Typanosoma cruzi* in the State of Rio de Janeiro, Brazil (Hemiptera, Reduviidae, Triatominae). *Mem. Inst. Oswaldo Cruz* 93:141-43
  153. Pinto C. 1939. Disseminação da malaria pela aviação; biologia do *Anopheles gambiae* e outros anophelíneos do Brasil. *Mem. Inst. Oswaldo Cruz* 34:293-430
  154. Pratt JJ, Hetrick RH, Harrison JB, Haber L. 1946. Tires as a factor in the transportation of mosquitoes by ships. *Mil. Surgeon* 99:785-88
  155. Provost MW. 1951. The occurrence of salt marsh mosquitoes in the interior of Florida. *Fla. Entomol.* 34:48-53
  156. Reiter P. 1998. *Aedes albopictus* and world trade in used tires, 1988-1995: the shape of things to come? *J. Am. Mosq. Control Assoc.* 14:83-94
  157. Reiter P, Darsie RF. 1984. *Aedes albopictus* in Memphis, Tennessee (USA): an achievement of modern transportation? *Mosq. News* 44:396-99
  158. Restifo RA, Lanzaro GC. 1980. The occurrence of *Aedes atropalpus* (Coquillett) breeding in tires in Ohio and Indiana. *Mosq. News* 40:292-94
  159. Richardson DM, Pysek P, Rejmánek M, Barbour MG, Panetta FD, et al. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.* 6:93-107
  160. Rodhain F, Charmot G. 1982. Evaluation des risques de reprise de transmission du paludisme en France. *Med. Mal. Infect.* 12:231-36
  161. Rodrigues da Silva G, Litvoc J, Goldbaum M, Dias JCP. 1979. Aspectos da epidemiologia da doença de Chagas. *Cienc. Cult.* 31(Suppl.):81-103
  162. Romi R, DiLuca M, Majori G. 1999. Current status of *Aedes albopictus* and *Aedes atropalpus* in Italy. *J. Am. Mosq. Control Assoc.* 15:425-27
  163. Romi R, Sabatinelli G, Giannuzzi Savelli L, Raris M, Zago M, et al. 1997. Identification of a North American species, *Aedes atropalpus* (Diptera: Culicidae) in Italy. *J. Am. Mosq. Control Assoc.* 13:245-46
  164. Rosci MA, Paglia MG, DeFelici A, Antonucci G, Armignacco U, et al. 1987. A case of falciparum malaria acquired in Italy. *Trop. Geogr. Med.* 39:77-79
  165. Rosen L, Rozeboom LE, Reeves WC, Saugrain J, Gubler DJ. 1976. A field trial of competitive displacement of *Aedes polynesiensis* by *Aedes albopictus* on a Pacific atoll. *Am. J. Trop. Med. Hyg.* 25:906-13
  166. Ross HH. 1964. The colonization of temperate North America by mosquitoes and man. *Mosq. News* 24:103-8
  167. Ross R. 1910. *The Prevention of Malaria*. New York: Dutton. 711 pp.
  168. Rossi GC, Pascual NT, Krsticevic FJ. 1999. First record of *Aedes albopictus* (Skuse) from Argentina. *J. Am. Mosq. Control Assoc.* 15:422
  169. Rozendaal JA. 1992. Relations between *Anopheles darlingi* breeding habitats, rainfall, river level and malaria transmission rates in the rain forest of Suriname. *Med. Vet. Entomol.* 6:16-22
  170. Russell RC. 1987. Survival of insects in the wheel bays of a Boeing 747B aircraft on flights between tropical and temperate airports. *Bull. WHO* 65:659-62

171. Russell RC. 1989. Transport of insects of public health importance on international aircraft. *Trav. Med. Intern.* 7:26-31
172. Russell RC, Paton R. 1989. In-flight disinsection as an efficacious procedure for preventing international transport of insects of public health importance. *Bull. WHO* 67:543-47
173. Russell RC, Rajapaska N, Whelan PI, Langsford WA. 1984. Mosquito and other introductions to Australia aboard international aircraft, and the monitoring of disinsection procedures. See Ref. 97, pp. 109-41
174. Sabatini A, Raineri V, Trovato G, Coluzzi M. 1990. *Aedes albopictus* in Italia e possibile diffusione della specie nell'area mediterranea. *Parassitologia* 32:301-4
175. Savage HM, Ezike VI, Nwankwo CAN, Spiegel R, Miller BR. 1992. First record of breeding populations of *Aedes albopictus* in continental Africa: implications for arboviral transmission. *J. Am. Mosq. Control Assoc.* 8:101-3
176. Schofield CJ. 1988. Biosystematics of the Triatominae. In *Biosystematics of Haematophagous Arthropods*, ed. MW Service, pp. 284-312. Oxford, UK: Clarendon
177. Schofield CJ, Dujardin J. 1999. Theories on the evolution of *Rhodnius*. *Actual. Biol. (Medellin)* 71:183-97
178. Schofield CJ, Matthews JNS. 1985. Theoretical approach to active dispersal and colonization of houses by *Triatoma infestans*. *J. Trop. Med. Hyg.* 88:211-22
179. Sellers RF. 1992. Weather, *Culicoides*, and the distribution and spread of bluetongue and African horse sickness viruses. In *Bluetongue, African Horse Sickness, and Related Orbiviruses*, Proc. Sec. Intern. Symp., ed. TE Walton, BI Osburn, pp. 284-90. Boca Raton, FL: CRC. 1042 pp.
180. Serufo JC, Oca HM, Tavares VA, Souza AM, Rosa RV, et al. 1993. Isolation of dengue virus type 1 from larvae of *Aedes albopictus* in Campos Altos city, State of Minas Gerais, Brazil. *Mem. Inst. Oswaldo Cruz* 88:503-4
181. Shaffner F, Carch S. 2000. First report of *Aedes albopictus* (Skuse, 1894) in Metropolitan France. *Compt. Rend. Acad. Sci. Fr. Ser. III, Sci. Vie* 323:373-75
182. Shigesada N, Kawasaki K. 1997. *Biological Invasions: Theory and Practice*. New York: Oxford. 205 pp.
183. Shroyer DA. 1981. Establishment of *Wyeomyia mitchellii* on the island of Oahu, Hawaii. *Mosq. News* 41:805-6
184. Deleted in proof
185. Simberloff D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pac. Sci.* 49:87-97
186. Simberloff D. 1997. The biology of invasions. See Ref. 187, pp. 1-17
187. Simberloff D, Schmitz DC, Brown TC, eds. 1997. *Strangers in Paradise. Impact and Management of Nonindigenous Species in Florida*. Washington, DC: Island. 467 pp.
188. Smith A, Carter ID. 1984. International transportation of mosquitoes of public health importance. See Ref. 97, pp. 1-21
189. Smith CEG. 1956. The history of dengue in tropical Asia, and its probable relationship to the mosquito *Aedes aegypti*. *J. Trop. Med. Hyg.* 59:3-11
190. Soper FL. 1965. The 1964 status of *Aedes aegypti* eradication and yellow fever in the Americas. *Am. J. Trop. Med. Hyg.* 14:887-91
191. Soper DL, Wilson DB. 1943. *Anopheles gambiae* in Brazil 1930 to 1940. New York: Rockefeller Found. 262 pp.
192. Sota T. 1994. Larval diapause, size, and autogeny in the mosquito *Aedes togoi* (Diptera, Culicidae) from tropical to subarctic zones. *Can. J. Zool.* 72:1462-68
193. Sprenger D, Wuithiranyagool T. 1986. The discovery and distribution of *Aedes albopictus* in Harris County, Texas,



- USA. *J. Am. Mosq. Control Assoc.* 2:217-19
194. Steffan WA. 1968. Hawaiian *Toxorhynchites* (Diptera: Culicidae). *Proc. Hawaii Entomol. Soc.* 20:141-55
195. Stojanovich CJ, Scott HG. *Mosquitoes of Italy*. USA: Self-published. 200 pp.
196. Symes GB. 1936. Insects in aeroplanes. *Q. Bull. Health Org. Leag. Nat.* 5:79-86
197. Tabachnick WJ. 1991. Evolutionary genetics and arthropod-borne disease. The yellow fever mosquito. *Am. Entomol.* 37:14-24
198. Tanaka K, Mizusawa K, Saugstad ES. 1979. A revision of the adult and larval mosquitoes of Japan (including the Ryukyu Archipelago and the Ogasawara Islands) and Korea (Diptera: Culicidae). *Contrib. Am. Entomol. Inst.* 16(1):1-987
199. Taylor RM. 1951. Epidemiology. In *Yellow Fever*, ed. GK Strode, pp. 431-538. New York: McGraw-Hill. 710 pp.
200. Teesdale C. 1950. An apparent invasion of *Aedes (Banksinella) lineatopenis* and *Aedes (B.) albicosta* into Mombasa Island. *Proc. R. Entomol. Soc. London Ser. A* 25:99-102
201. Turell MJ, O'Guinn ML, Dohm DJ, Jones JW. 2001. Vector competence of North American mosquitoes (Diptera: Culicidae) for West Nile virus. *J. Med. Entomol.* 3:130-34
202. Urbanelli S, Bellini R, Carrieri M, Sallicandro P, Celli G. 2000. Population structure of *Aedes albopictus* (Skuse): the mosquito which is colonizing Mediterranean countries. *Heredity* 84:331-37
203. Van Driesche RG, Bellows TS. *Biological Control*. New York: Chapman & Hall. 539 pp.
204. Van Riper C, Van Riper SG, Goff ML, Laird M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56:327-44
205. Vermeij G. 1996. An agenda for invasion biology. *Biol. Conserv.* 78:3-9
206. Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R. 1996. Biological invasions as global environmental change. *Am. Sci.* 84:468-78
207. Walsh JF, Davies JB, Cliff B. 1981. World Health Organization Onchocerciasis Control Programme in the Volta River Basin. In *Blackflies: The Future for Biological Methods in Integrated Control*, ed. M. Laird, pp. 85-103. New York: Academic. 399 pp.
208. Ward RA. 1984. Mosquito fauna of Guam: case history of an introduced fauna. See Ref. 97, pp. 143-62
209. Washburn JO, Hartmann EU. 1992. Could *Aedes albopictus* (Diptera: Culicidae) become established in California treeholes? *J. Med. Entomol.* 29:995-1005
210. Weinstein P, Laird M, Browne G. 1997. *Exotic and Endemic Mosquitoes in New Zealand As Potential Arbovirus Vectors*. Wellington, UK: Minist. Health. 16 pp.
211. Whelan P, Hayes G, Tucker G, Carter J, Wilson A, et al. 2001. The detection of exotic mosquitoes in the Northern Territory of Australia. *Arbovirus Res. Aust.* 8:395-404
212. White DJ, White CP. 1980. *Aedes atropalpus* breeding in artificial containers in Suffolk County, New York. *Mosq. News* 40:106-7
213. White GB. 1985. Airport malaria and jumbo vector control. *Parasitol. Today* 1:177-79
214. Whitfield FGS. 1940. Air transport, insects and disease. *Bull. Entomol. Res.* 3:365-442
215. Wigglesworth VB. 1965. *The Principles of Insect Physiology*. London: Methuen. 741 pp. 6th ed.
216. Williams CL. 1940. Disinsectization of aircraft. *Public Health Rep.* 55:1005-10
217. Williamson M. 1992. Environmental risks from the release of genetically modified organisms (GMOs)—the need

- for molecular ecology. *Mol. Ecol.* 1:3–8
218. Williamson M. 1993. Invaders, weeds and the risk from genetically modified organisms. *Experientia* 49:219–24
219. Williamson M. 1996. *Biological Invasions*. New York: Chapman & Hall. 244 pp.
220. Williamson M. 1999. Invasions. *Ecography* 22:5–12
221. Williamson M, Fitter A. 1996. The varying success of invaders. *Ecology* 77: 1661–66
222. Zavortink TJ. 1972. Mosquito studies (Diptera, Culicidae) XXVIII. The New World species formerly placed in *Aedes* (*Finlaya*). *Contrib. Am. Entomol. Inst.* 8(3):1–206
223. Zavortink TJ, O'Meara GF. 1999. *Culex* (*Micraedes*) *biscaynensis* n. sp. from Florida (Diptera: Culicidae). *J. Am. Mosq. Control. Assoc.* 15:263–70
224. Zeledón R. 1972. Los vectores de la enfermedad de Chagas en America. In *Simposio Internacional sobre Enfermedad de Chagas*, pp. 327–45. Buenos Aires: Soc. Argent. Parasitol.



## CONTENTS

---

ROSS RIVER VIRUS: ECOLOGY AND DISTRIBUTION, <i>Richard C. Russell</i>	1
BIOLOGY AND MANAGEMENT OF THE SMOKYBROWN COCKROACH, <i>Arthur G. Appel and Lane M. Smith II</i>	33
SEQUESTRATION OF DEFENSIVE SUBSTANCES FROM PLANTS BY LEPIDOPTERA, <i>Ritsuo Nishida</i>	57
REGULATION OF DIAPAUSE, <i>David L. Denlinger</i>	93
BACTERIAL SYMBIONTS OF THE TRIATOMINAE AND THEIR POTENTIAL USE IN CONTROL OF CHAGAS DISEASE TRANSMISSION, <i>C. Ben Beard,</i> <i>Celia Cordon-Rosales, and Ravi V. Durvasula</i>	123
STRATEGIES AND STATISTICS OF SAMPLING FOR RARE INDIVIDUALS, <i>Robert C. Venette, Roger D. Moon, and William D. Hutchison</i>	143
BIOLOGY AND MANAGEMENT OF THE JAPANESE BEETLE, <i>Daniel A.</i> <i>Potter and David W. Held</i>	175
BIOLOGY AND ECOLOGY OF HIGHER DIPTERA FROM FRESHWATER WETLANDS, <i>Joe B. Keiper, William E. Walton, and Benjamin A. Foote</i>	207
INVASIONS BY INSECT VECTORS OF HUMAN DISEASE, <i>L. Philip Lounibos</i>	233
OMNIVORY IN TERRESTRIAL ARTHROPODS: MIXING PLANT AND PREY DIETS, <i>Moshe Coll and Moshe Guershon</i>	267
HOW TO BE A FIG WASP, <i>George D. Weiblen</i>	299
ALTERNATIVES TO METHYL BROMIDE TREATMENTS FOR STORED-PRODUCT AND QUARANTINE INSECTS, <i>Paul G. Fields</i> <i>and Noel D. G. White</i>	331
ECOLOGY AND BEHAVIOR OF FIRST INSTAR LARVAL LEPIDOPTERA, <i>Myron P. Zalucki, Anthony R. Clarke, and Stephen B. Malcolm</i>	361
ARTHROPOD ALLERGENS AND HUMAN HEALTH, <i>Larry G. Arlian</i>	395
COMPETITIVE DISPLACEMENT AMONG INSECTS AND ARACHNIDS, <i>Stuart R. Reitz and John T. Trumble</i>	435
ENDOCRINE INSIGHTS INTO THE EVOLUTION OF METAMORPHOSIS IN INSECTS, <i>James W. Truman and Lynn M. Riddiford</i>	467
BIOCHEMISTRY AND GENETICS OF INSECT RESISTANCE TO <i>BACILLUS THURINGIENSIS</i> , <i>Juan Ferré and Jeroen Van Rie</i>	501

IRON METABOLISM IN INSECTS, <i>Helen Nichol, John H. Law, and Joy J. Winzerling</i>	535
CAN GENERALIST PREDATORS BE EFFECTIVE BIOCONTROL AGENTS?, <i>W. O. C. Symondson, K. D. Sunderland, and M. H. Greenstone</i>	561
ARTHROPODS ON ISLANDS: COLONIZATION, SPECIATION, AND CONSERVATION, <i>Rosemary G. Gillespie and George K. Roderick</i>	595
THE POPULATION BIOLOGY OF OAK GALL WASPS (HYMENOPTERA: CYNIPIDAE), <i>Graham N. Stone, Karsten Schönrogge, Rachel J. Atkinson, David Bellido, and Juli Pujade-Villar</i>	633
SHORT, LONG, AND BEYOND: MOLECULAR AND EMBRYOLOGICAL APPROACHES TO INSECT SEGMENTATION, <i>Gregory K. Davis and Nipam H. Patel</i>	669
BIOLOGY AND MANAGEMENT OF ECONOMICALLY IMPORTANT LEPIDOPTERAN CEREAL STEM BORERS IN AFRICA, <i>Rami Kfir, W. A. Overholt, Z. R. Khan, and A. Polaszek</i>	701
THE ECOLOGY AND EVOLUTION OF ANT ASSOCIATION IN THE LYCAENIDAE (LEPIDOPTERA), <i>Naomi E. Pierce, Michael F. Braby, Alan Heath, David J. Lohman, John Mathew, Douglas B. Rand, and Mark A. Travassos</i>	733
SYMPATRIC SPECIATION IN PHYTOPHAGOUS INSECTS: MOVING BEYOND CONTROVERSY?, <i>Stewart H. Berlocher and Jeffrey L. Feder</i>	773
HOST PLANT QUALITY AND FECUNDITY IN HERBIVOROUS INSECTS, <i>Caroline S. Awmack and Simon R. Leather</i>	817
ECONOMIC, ECOLOGICAL, FOOD SAFETY, AND SOCIAL CONSEQUENCES OF THE DEPLOYMENT OF BT TRANSGENIC PLANTS, <i>A. M. Shelton, J.-Z. Zhao, and R. T. Roush</i>	845
CONTROL AND BIOCHEMICAL NATURE OF THE ECDYSTEROIDOGENIC PATHWAY, <i>Lawrence I. Gilbert, Robert Rybczynski, and James T. Warren</i>	883
THE BIOLOGY OF THE DANCE LANGUAGE, <i>Fred C. Dyer</i>	917
INDEXES	
Subject Index	951
Cumulative Index of Contributing Authors, Volumes 38–47	987
Cumulative Index of Chapter Titles, Volumes 38–47	991

## ERRATA

An online log of corrections to *Annual Review of Entomology* chapters may be found at <http://ento.AnnualReviews.org/errata.shtml>