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SUPPLEMENT ARTICLE

# Invasiveness of *Aedes aegypti* and *Aedes albopictus* and Vectorial Capacity for Chikungunya Virus

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In this review, we highlight biological characteristics of *Aedes aegypti* and *Aedes albopictus*, 2 invasive mosquito species and primary vectors of chikungunya virus (CHIKV), that set the tone of these species' invasiveness, vector competence, and vectorial capacity (VC). The invasiveness of both species, as well as their public health threats as vectors, is enhanced by preference for human blood. Vector competence, characterized by the efficiency of an ingested arbovirus to replicate and become infectious in the mosquito, depends largely on vector and virus genetics, and most *A. aegypti* and *A. albopictus* populations thus far tested confer vector competence for CHIKV. VC, an entomological analog of the pathogen's basic reproductive rate ($R_0$), is epidemiologically more important than vector competence but less frequently measured, owing to challenges in obtaining valid estimates of parameters such as vector survivorship and host feeding rates. Understanding the complexities of these factors will be pivotal in curbing CHIKV transmission.

**Keywords.** *Aedes aegypti*; *Aedes albopictus*; chikungunya; competitive displacement; invasiveness; satyrization; vectorial capacity; vector competence.

Because most cases of chikungunya fever arise as a consequence of infectious bites by either of the mosquito species *Aedes aegypti* or *Aedes albopictus*, this review synthesizes aspects of the biology of these species that contribute to their public health threats. Both species are highly invasive, so we begin by considering features of *A. aegypti* and *A. albopictus* that have enabled their establishment in human-dominated environments across the globe. The second section of this contribution focuses on vectorial capacity (VC), namely the biological characteristics of females of these species that facilitate their infection by, replication of, and transmission of chikungunya viruses.

## ATTRIBUTES OF INVASIVENESS

Invasion biology studies the introduction, establishment, and spread of nonnative species outside their native ranges. In this review, we distinguish invasive species from other nonnative species on the basis of their impacts. Particularly, invasive species, in contrast to other nonnative species, are of greater concern because of their realized or potential effects on native species and ecosystems and/or human activities and health [1].

A previous review distinguished between 9 invasive mosquitoes and 22 other, nonnative species that have become established outside their native ranges [1]. These 31 species combined were significantly more likely than mosquitoes that have not expanded their ranges to have drought-resistant eggs, presumably because this trait has enabled their transport and introduction into new regions; however, the proportions of invasive and nonnative species with this trait did not differ significantly (Table 1). Although larval development in container habitats did not differ significantly between invasive and nonnative mosquito species, significantly more invasive mosquito species than nonnative species were associated with human-dominated habitats (Table 1).

Considering invasive animals and plants associated with human environments, Hufbauer et al [2] proposed that preadaptations in their native ranges predispose such species for future success in invaded environments. The anthropogenically induced adaptation to invade hypothesis of Hufbauer et al [2] has been applied to *A. aegypti* and *A. albopictus* to account for the invasive success of these vector species [3].

In its native range in Africa, *A. aegypti* is recognized as occurring in 2 forms, a feral morph sometimes recognized as subspecies *formosus*, and a domesticated form, subspecies *aegypti* [4]. Globally widespread by shipping in previous centuries [5], the majority of successful invasive establishments of *A. aegypti*, especially in tropical regions of Asia and the Americas, are genetically more closely related to the domestic morph [6], with accompanying adaptations such as preferences for human blood and occupancy of man-made containers in their immature stages [4].

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**Table 1. Associations of Biological Traits With Invasiveness Among Mosquito Species**

| | Invasive Species | | Other Nonnative Species | | All Other Culicidae | | |
|---|---|---|---|---|---|---|---|
| Biological Trait | + | – | + | – | + | – | *P* Value[a] |
| Desiccation-resistant eggs | 5 | 4 | 14 | 8 | 1012 | 2479 | .002 |
| Desiccation-resistant eggs | 5 | 4 | 14 | 8 | . . . | . . . | .693 |
| Container larval microhabitat | 7 | 2 | 10 | 12 | . . . | . . . | .134 |
| Human-dominated macrohabitat | 6 | 3 | 3 | 19 | . . . | . . . | .028 |

Data are modified from [1].

Abbreviations: +, presence of trait; –, absence of trait.

[a] By the Fisher exact test. The value in the first row is for the comparison of invasive species plus other nonnative species to all other Culicidae, whereas values in remaining rows are for comparisons of invasive species to other nonnative species.

The feral morph *A. aegypti formosus* preferentially occupies ecotonal, disturbed habitats on the Kenyan coast [7], which may have predisposed this species for subsequent domestic adaptations within Africa, as hypothesized by Tabachnick [8]. In its native Asian range, *A. albopictus* is also ecotonal, occurring preferentially on forest fringes, which is the habitat preference also observed in its invasive range [9] and has probably contributed to its invasive success worldwide [3].

## FURTHER ADAPTATIONS FAVORING INVASIVENESS

### Reproductive Competition and Character Displacement

The arrival and spread of *A. albopictus* in the southeastern United States, in the 1980s, were associated with rapid reductions and displacements of the resident container mosquito species, *A. aegypti* [10]. A similarly speedy competitive reduction of *A. aegypti* by *A. albopictus* in Bermuda was witnessed in the early 2000s by Kaplan et al [11]. Possible displacements of *A. aegypti* by *A. albopictus* have also been reported from central Africa [12] and Reunion and Mayotte islands in the Indian Ocean [13, 14].

Although the superiority of *A. albopictus* over *A. aegypti* in larval competition in resource-limited environments was formerly proposed as the most likely causal mechanism for observed displacements [5], recently a form of asymmetric reproductive interference, satyrization, has been proposed as a more likely cause of the rapid displacements and reductions of *A. aegypti* [15]. Interspecific matings between these species occur in nature wherever their ranges overlap but yield no offspring, and *A. aegypti* populations are affected more deleteriously by the errant matings than *A. albopictus*. This is because virgin female *A. aegypti* but not *A. albopictus* females are sterilized by accessory gland substances from heterospecific males [15]. Satyrization has been suggested to be an adaptation, or exaptation (a nonadaptive change), favoring the invasive success of *A. albopictus* [16].

In response to satyrization by *A. albopictus*, populations of *A. aegypti* in nature have evolved resistance to reproductive competition via character displacement, which favors coexistence of the two species by reducing the frequencies of cross-matings [16, 17]. Selection for satyrization resistance in *A. aegypti* is accompanied by fitness costs in laboratory populations, such as reduced fecundity and slower time to mating with members of their own species [16]. These costs probably account for the low levels of interspecific mating still observed in sympatric populations of these species in nature [16].

### Anthropophily

In keeping with its preferred occupancy of urban environments, most invasive populations of domestic *A. aegypti* feed predominantly on human blood, which facilitates its vectoring of arboviruses in human-mosquito cycles in the absence of zoonotic reservoirs [18]. Similar to endophilic malaria vector species in Africa, domestic *A. aegypti* may often consume blood multiple times per gonotrophic cycle, thereby increasing its potential as an arbovirus vector [18].

In contrast, *A. albopictus* preferentially occurs in vegetated and rural habitats, especially where it is sympatric with *A. aegypti* [19]. However, when *A. aegypti* is absent, this species can be highly productive in urban habitats [20]. *A. albopictus* has been regarded traditionally as a mammal-feeding generalist [19], but at many locations in its native and invasive ranges, humans account for the preponderance of blood meals identified from engorged specimens collected in nature (Table 2). Host-choice experiments on female *A. albopictus* from Reunion Island, where this species transmitted chikungunya virus (CHIKV) during the 2006–2007 southwestern Indian Ocean epidemic, showed the local population to prefer humans above all alternative blood-meal hosts [30].

## VECTORIAL CAPACITY

Viruses transmitted by *A. aegypti* and *A. albopictus* cause some of the most significant arthropod-borne viral diseases in the world, including the flaviviruses yellow fever virus (YFV), dengue virus (DENV), and Zika virus (ZIKV) and the alphavirus CHIKV. There are many reasons why these 2 mosquito species present such a great public health threat. Among these are environmental, behavioral, and genetic components. The threat to public health posed by *A. aegypti* in particular and

**Table 2. Anthropophily of *Aedes albopictus*, Based on Identifications of Blood-Meal Hosts of Wild-Caught Females of this Species**

| Country | Habitat | Number of Bloodmeal Identifications | Human Host, % of Feeding Episodes | Reference |
|---|---|---|---|---|
| Japan | Suburban/urban | 114 | 68.5 | [21] |
| Thailand | Rural | 105 | 94.3 | [22] |
| China (Macau) | Rural | 48 | 63.9 | [23] |
| India | Suburban/urban | 534 | 99.5 | [24] |
| Singapore | Rural | 37 | 91.9 | [25] |
| Cameroon[a] | Rural | 170 | 100.0 | [26] |
| Italy[a] | Urban | 243 | 91.1 | [27] |
| Brazil[a] | Urban | 177 | 68.2 | [28] |
| USA(NJ)[a] | Urban | 86 | 68.8 | [29] |

Nonrandom examples of feeding predominantly on human hosts.

[a] Invasive range of this species.

*A. albopictus* less so is largely a consequence of their focused feeding on and close association with humans. Further facilitating viral spread is the ability of both the human host and mosquito vector to travel, the human actively and the mosquito more passively in immature stages, for example. Such a pattern is dangerous because it spreads viruses to new locations, hospitable to the vector, with naive human hosts. This section concentrates on selected components of virus-vector-vertebrate (human) interrelationships, focusing specifically on how interactions between vector, virus, and environment shape the patterns and intensity of transmission of one of the important viral pathogens mentioned above, CHIKV.

Mosquito-borne disease outbreaks are influenced by intrinsic (eg, vector and viral genetics, vector and host competence, and vector life-history traits) and extrinsic (eg, temperature, rainfall, and human land use) factors that affect virus activity and mosquito biology in complex and interconnected ways (Figure 1) [31]. Disease prevalence varies spatially and temporally, depending on VC, a concept that integrates intrinsic and extrinsic factors to address interactions of the virus with the arthropod and human host. VC leads to a clearer understanding of their complex interrelationships and how such relationships influence transmission of vector-borne pathogens. Determination of risk is measured through elucidation of the factors that compose VC. Other factors, such as human immune status and population density, also affect transmission dynamics, but they will not be discussed here. All of the contributing factors taken together have an impact on selective pressures shaping dynamic viral populations, host-virus outcomes, and, ultimately, epidemiological patterns.

VC is essentially an entomological restatement of the basic reproductive rate ($R_0$) of a pathogen, defined as the number of secondary infections expected to occur from the introduction of a single infection in a naive population. An equation formalizing VC was described by Macdonald [32] and later modified by others. One of these, described by Black and Moore [33], provides a useful platform for rational examination of selective forces that may shape *Aedes*-transmitted arboviruses. This formula is $VC = [ma^2 (I^*T)p^n]/-\ln(p)$, where $m$ is the vector density in relation to the host, $a$ is the probability that a vector feeds on a host in 1 day (ie, the host preference index multiplied by the feeding frequency), $p$ is the probability that a vector survives 1 day, $n$ is the duration of the extrinsic incubation period (EIP) in days, $I$ (infection rate) * $T$ (transmission rate) is equal to vector competence ($b$) or the proportion of vectors ingesting an infective meal that are later able to transmit the infection, and $1/-\ln(p)$ is the duration of the vector's life in days after surviving the EIP. This equation demonstrates that the abundance ($m$) and vector competence ($b$) of mosquito populations would influence the reproductive rate of the arbovirus linearly and, thus, relatively weakly. In contrast, host feeding ($a$), vector longevity ($p$), and EIP ($n$) would influence $R_0$ much more powerfully (eg, as a square or exponent). It seems to follow that virus infectivity for mosquitoes, which would be incorporated into VC as $b$, would be of relatively minor importance as compared to viral factors, such as the speed of dissemination from the midgut, that would impact the duration of the EIP, which would influence VC as $n$ [31]. Thus, natural selection might favor a poorly infectious but rapidly disseminating virus over a highly infectious virus that disseminates slowly. Similar predictions might be made about viral influences on other mosquito-associated factors, such as host preference and survivorship.

Frequency of feeding on the targeted host (host feeding [$a$]) is an important component of VC. As aforementioned, domestic *A. aegypti* feed predominantly on human blood [4, 22] and take multiple blood meals during each gonotrophic cycle [18]. Once female mosquitoes are infectious, they may transmit virus each time they probe or take a blood meal. Domestic *A. aegypti* live in close proximity to humans, where they may feed on blood frequently.

*A. albopictus* also may preferentially feed on humans, as previously stated (Table 2), but some populations of this species may be more opportunistic in their host preferences, feeding on a variety of mammalian and avian species if available [19]. *A. albopictus* also may be found in more-diverse environmental settings than *A. aegypti*, such as suburban and rural environments. However, in south Florida before *A. albopictus* arrived, *A. aegypti* could be found in rural environments. In southern China, outside the range of *A. aegypti*, *A. albopictus* is urban dwelling [20]. Therefore, the niche width of these 2 species is not absolute.

## VECTOR COMPETENCE

Even though vector competence is of relatively minor importance in the VC equation, where it is represented as a linear

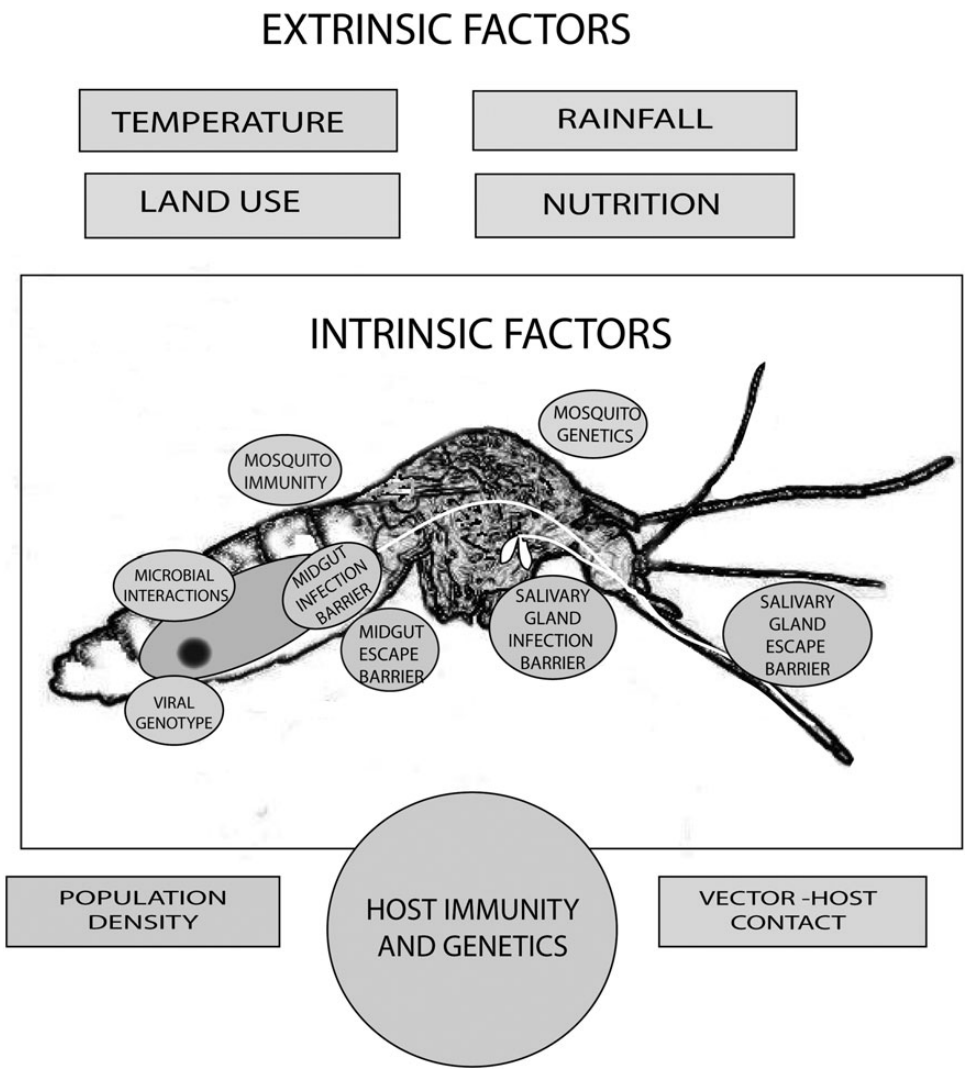


**Figure 1.** Factors affecting the vectorial capacity of a mosquito vector (modified from [31] with permission).

function, the mosquito must be physiologically competent for transmission to occur. That said, relatively incompetent vectors are capable of initiating and sustaining arbovirus outbreaks in the presence of high population density [34]. Such incompetence may actually select for higher viremia titers in the human host.

A competent mosquito is one in which virus (1) is ingested with the blood meal, (2) successfully infects and multiplies in mesenteronal epithelial cells, (3) disseminates to parenteral tissues where it replicates further, (4) infects salivary glands (or, alternatively, may infect salivary glands directly following release from the mesenteron), and (5) is released from the salivary gland epithelial cells into the salivary secretion and is transmitted during feeding (Figure 2) [35]. The susceptibility of a population is generally defined as the concentration of virus required to infect 50% of a mosquito population ($ID_{50}$). Both virus and vector genetics influence vector competence. With DENV, variation occurs in both interspecific and intraspecific serotype-specific $ID_{50}$ estimates. For example, the $ID_{50}$ for DENV-1 and DENV-2 was lower than for DENV-3 and DENV-4 in one study in Vietnam [36], and field populations of *A. aegypti* demonstrated lower vector competence for the American genotype of DENV-2 than the Southeast Asian genotype [37]. It has been shown that people with asymptomatic and presymptomatic DENV infections had an approximately 100-fold lower $ID_{50}$ and resulted in larger viral loads in infected mosquitoes, which was interpreted as increased transmission potential [38].

Transmission of East/Central/South African CHIKV by *A. albopictus* was facilitated after an amino acid change from alanine to valine at position 226 of CHIKV E1 glycoprotein (E1-A226 V), causing increased replication, midgut infection, dissemination, and transmission in this species, with no significant changes observed in *A. aegypti*'s competence [39].

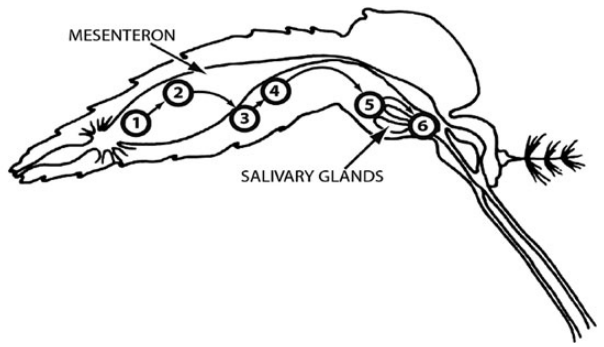


**Figure 2.** Sequential steps required for a competent female mosquito to transmit an arbovirus after ingestion of an infective blood meal (modified from [35] with permission).

This adaptive mutation enhancing the vector competence of *A. albopictus* is thought to have occurred on at least 3 independent occasions in the Indian Ocean region, the Indian subcontinent, and Central Africa, supporting the hypothesis of convergent evolution [40]. Additional adaptive mutations in CHIKV have been identified in *A. albopictus*. These are E2 substitutions, with 1 mutation also involving an E3 substitution [41]. As with the E1 mutation, these changes enhance initial infection of the mosquito midgut and have little, if any, effect on infection of *A. aegypti*.

Additionally, vector competence is a quantitative trait that has been found to be highly variable in wild populations of *A. aegypti* [42]. When *A. albopictus* transmission potential for CHIKV was measured in 6 worldwide vector populations, with 2 virus strains and in 2 ambient temperatures (20° and 28°C), strong effects of the 3-way interaction of mosquito population, virus strain, and temperature were observed. This highlights the importance of studies that focus on genotype by genotype by environment interactions [43]. Differences in transmission efficiency of CHIKV by *A. aegypti* and *A. albopictus* were noted in populations of both species from the Americas, while dissemination rates were similar. This confirms that salivary glands may act as an anatomical barrier to virus transmission and may vary with mosquito and viral genetics, as well as viral dose [44]. Nonetheless, transmission efficiency reached rates as high as 83% and 97% in *A. aegypti* and *A. albopictus* populations, respectively [45].

Composition of the midgut bacterial community also has an impact on vector competence. One study showed 10–100-fold higher bacterial abundance in midguts of a DENV-resistant strain of *A. aegypti* as compared to susceptible and unselected strains [46]. Another study demonstrated that regulation of genes in the innate immune pathway (Toll pathway) was stimulated by natural gut microbiota [47]. These investigators further showed that mosquitoes reared without the presence of endogenous bacterial flora were less responsive immunologically to DENV, which was present in midguts at 2-fold higher titers as compared to wild-type mosquitoes.

Insect-specific viruses (ie, RNA viruses that replicate only in insects and not in vertebrate hosts) also may affect vector competence. They represent a broad range of families, including *Flaviviridae* and *Togaviridae*. It is suspected that competitive inhibition may diminish competence for some but not all secondarily infecting arboviruses [48].

Environmental or abiotic factors may have large effects on vector competence and VC. The climatic suitability for CHIKV and DENV outbreaks is dependent on bioclimatic factors that influence both vector and virus. Temperature is recognized to have a stronger influence on *A. albopictus* abundance than precipitation [49], but low rainfall levels may lead to an extinction of the *A. albopictus* population [50]. In a study that evaluated the impact of diurnal temperature range, *A. aegypti* lived longer and was more likely to become infected under moderate temperature fluctuations, typical of the high DENV transmission season, than under large temperature fluctuations, typical of the low DENV transmission season [51]. Temperature also may affect critical components of VC, such as mosquito developmental time and consequent population density, survivorship, blood feeding, fecundity, and the EIP. This points to the complexity of understanding the dynamics of transmission of arthropod-borne diseases.

## CONCLUSIONS

CHIKV is now widespread worldwide and likely will continue to pose a public health threat globally wherever the invasive mosquitoes *A. albopictus* and *A. aegypti* are present and a naive human population exists. The biology of these 2 vectors makes them extremely difficult to control, and there is currently no Food and Drug Administration–approved vaccine to prevent disease. Several innovative approaches to vector control are in trial, one being population replacement with *Wolbachia*-infected *A. aegypti*. These mosquitoes have shorter life spans and high resistance to DENV, CHIKV, and YFV infection, and the intracellular *Wolbachia* bacteria remains established in the population [52]. However, *A. albopictus* is unaffected by this technique. An alternative, population-suppression approach being tested is release of male mosquitoes carrying dominant lethal genes [53]. At this time, basic personal measures are the most effective for prevention of CHIKV (eg, removal of standing water around homes and individual protection against mosquito bites). Important questions remaining to assist in control include further elucidation of the biology of *A. aegypti* and *A. albopictus*, increased understanding of the ecology and evolution of CHIKV in its natural setting, and evaluation of the potential for CHIKV to become enzootic outside its native range in Africa.

### Notes

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