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► **To cite this version:**

Pei-Shi Yen, Fadila Amraoui, Anubis Vega R  , Anna-Bella Failloux. *Aedes aegypti* mosquitoes from Guadeloupe (French West Indies) are able to transmit yellow fever virus. PLoS ONE, 2018, 13 (9), pp.e0204710. 10.1371/journal.pone.0204710 . pasteur-01887187

HAL Id: pasteur-01887187

<https://pasteur.hal.science/pasteur-01887187>

Submitted on 3 Oct 2018

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RESEARCH ARTICLE

Aedes aegypti mosquitoes from Guadeloupe (French West Indies) are able to transmit yellow fever virus

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OPEN ACCESS

Citation: Yen P-S, Amraoui F, Vega Rúa A, Failloux A-B (2018) *Aedes aegypti* mosquitoes from Guadeloupe (French West Indies) are able to transmit yellow fever virus. PLoS ONE 13(9): e0204710. <https://doi.org/10.1371/journal.pone.0204710>

Editor: Luciano Andrade Moreira, Centro de Pesquisas René Rachou, BRAZIL

Received: July 23, 2018

Accepted: September 12, 2018

Published: September 28, 2018

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Data Availability Statement: All relevant data are within the manuscript.

Funding: ABF was funded by French Government's Investissement d'Avenir program, Laboratoire d'Excellence "Integrative Biology of Emerging Infectious Diseases" (grant n°ANR-10-LABX-62-IBED); AVR was funded by FEDER grant that financed by the European Union and Guadeloupe Region, Programme Opérationnel FEDER-Guadeloupe-Conseil Régional 2014-2020 (Grant number 2015-FED-192). P-SY was supported by

Abstract

The recent yellow fever epidemic in Brazil has raised the concern of outbreaks in neighboring countries, particularly in the Caribbean region where the vector *Aedes aegypti* is predominant. This threat comes from the past when in the Americas, this disease caused devastating urban epidemics. We report the vector competence of *Ae. aegypti* from Guadeloupe for yellow fever virus by determining different parameters describing virus infection, dissemination, and transmission. The results indicate that *Ae. aegypti* Guadeloupe are susceptible to yellow fever virus with viral particles detected in mosquito saliva at 14 and 21 days post-infection. Local authorities and more broadly, international organizations should maintain the active surveillance of *Aedes* mosquitoes and the spreading of human cases from South America.

Introduction

Yellow fever (YF) is a mosquito-borne viral disease endemic to some countries of South America and sub-Saharan Africa. It can present various clinical features ranging from a self-limited, mild febrile illness to fatal symptoms such as hemorrhages and liver damages. Most of all cases reported annually (80–90%) occur in Africa where YF covers 44 countries [1]. In South America, YF is described in less than 10 countries: Argentina, Bolivia, Brazil, Colombia, Ecuador, Paraguay, Peru, and Venezuela (http://ais.paho.org/phis/viz/ed_yellowfever.asp). In these locations, YF uses to periodically spread via epizootic outbreaks following the displacements of non-human primates [2]. From July 2017 through March 2018, the states of Rio de Janeiro, Minas Gerais, and São Paulo in Brazil, counted 932 human cases including 300 fatal cases [3]. Alarmingly, human cases were reported near São Paulo city, threatening the initiation of an urban transmission that has not been notified in the country since 1942.

Originally from Africa, YF is believed to be introduced into America via the slave trade in the middle of 18th century [4]. Approximately 10.7 million slaves were deported to the Caribbean, North and South Americas during four centuries [5]. Likewise, the mosquito

the Institut Pasteur and the National Health Research Institutes in Taiwan. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Ae. aegypti by finding suitable breeding sites in slave transport ships, was introduced in America at the same period [6]. Deadly YF epidemics devastated the continent for centuries. An eradication campaign targeting *Ae. aegypti* organized by the Pan American Health Organisation (PAHO) was initiated in 1946 and led to the elimination of the vector from most American countries, and consequently, the disappearance of urban YF [7]. Unfortunately, the eradication campaign was interrupted and most countries were re-infested by the vector [8].

Yellow fever virus (YFV; *Flavivirus*, Flaviviridae) is primarily transmitted by the mosquitoes *Aedes* spp. (e.g. *Aedes africanus*) in Africa and *Haemagogus* (e.g. *Haemagogus janthinomys*) in South America [9]. In Brazil, the anthropophilic mosquitoes *Ae. aegypti* and *Aedes albopictus* as well as the YFV-enzootic mosquitoes *Haemagogus leucocelaenus* and *Sabethes albiprivus* are highly susceptible to YFV [10]. Thus, the widely distributed *Ae. aegypti* in American countries raises the concern of a re-urbanization of YF if the virus is introduced via viremic vertebrate hosts. In the Caribbean, Guadeloupe Island has experienced several outbreaks caused by arboviruses such as dengue [11], chikungunya [12] and zika [13], all three viruses only be transmitted by *Ae. aegypti* as *Ae. albopictus* is absent from the island [14]. To be considered as an epidemic vector of YFV, *Ae. aegypti* should be experimentally susceptible to the virus (i.e. a competent vector) in addition of being an anthropophilic mosquito [15] in close contacts with humans [16]. In this report, we evaluate the vector competence of *Ae. aegypti* from Guadeloupe to YFV. These results will help the local health authorities and the decision-makers to anticipate the arrival of YF in the Caribbean.

Materials and methods

Virus strain

The strain IEC-4408 (YFV-4408; accession number: KY861728) belonging to the 1E lineage of YFV, was isolated from a Howler monkey in 2008 [10]. The strain was passaged four times on *Ae. albopictus* C6/36 cells. Viral stocks for mosquito infections were produced on C6/36 cells and stored at -80°C.

Artificial blood feeding

Six boxes of 60 7-day-old F1 female adults (F0 collected as larvae in June 2017 in Deshaies, Basse Terre, Guadeloupe) were fed on an infectious blood meal containing 1.4 mL of washed rabbit red blood cells and 0.7 mL of virus suspension. The blood meal supplemented with ATP as a phagostimulant at a final concentration of 1 mM was provided to mosquitoes at a titer of $10^{6.5}$ focus-forming unit (ffu)/mL using a Hemotek membrane feeding system. Engorged mosquitoes were transferred into boxes and maintained with 10% sucrose at 28°C under a photoperiod of 12:12.

Mosquito sampling and processing

Mosquitoes were examined at 7, 14, and 21 days post-infection (dpi). After removing mosquito wings and legs, the proboscis was inserted into a P20 tip filled with 5 µL of fetal bovine serum (FBS) [17]. After 30 min, saliva was expelled from the tip to 45 µL of L-15 medium (Invitrogen, California, USA) and then processed for viral titration to estimate transmission. Then, mosquito head and body were collected and ground individually in 300 µL of L-15 medium supplemented with 2% FBS, for respectively, viral infection and dissemination analysis. 200 µL of homogenates were collected after centrifugation at 10,000 g for 5 min at +4°C before viral titration. To estimate the vector competence, three parameters were calculated: (i) infection

rate (IR) referring to the proportion of mosquitoes with infected body among engorged mosquitoes, (ii) dissemination rate (DR) corresponding to the proportion of mosquitoes with infected head among mosquitoes with infected body, and (iii) transmission rate (TR) representing the proportion of mosquitoes with infectious saliva among mosquitoes with infected head.

Virus titration

Mosquito samples were titrated by focus fluorescent assay on *Ae. albopictus* C6/36 cells in 96-well plates [18]. After 5 days of incubation at 28°C, plates were stained using antibodies specific to YFV as the primary antibody and conjugated Alexa Fluor 488 goat anti-mouse IgG as the second antibody (Life Technologies, California, USA).

Statistical analysis

Statistical analyses were performed with Stata software (StataCorp LP, Texas, and USA). P-values < 0.05 were considered significant.

Results

Mosquitoes were analyzed at three time points following infection: 7, 14 and 21 days post infection (dpi). At 7 dpi, 56.7% (17/30) of mosquitoes examined had infected bodies (Fig 1). Among them, 29.4% (5/17) of mosquitoes were able to ensure a viral dissemination beyond the midgut barrier in the hemocele. No mosquitoes were able to transmit the virus with no viral particles detected in mosquito saliva. Later, at 14 dpi, a higher proportion, 70% (21/30) of mosquitoes had an infected body and among them, 57.1% (12/21) presented a positive viral dissemination into the hemocele. Then, 8.3% (1/12) had virus in saliva, indicative of viral transmission; one mosquito had 20 viral particles. At 21 dpi, the proportion of mosquitoes

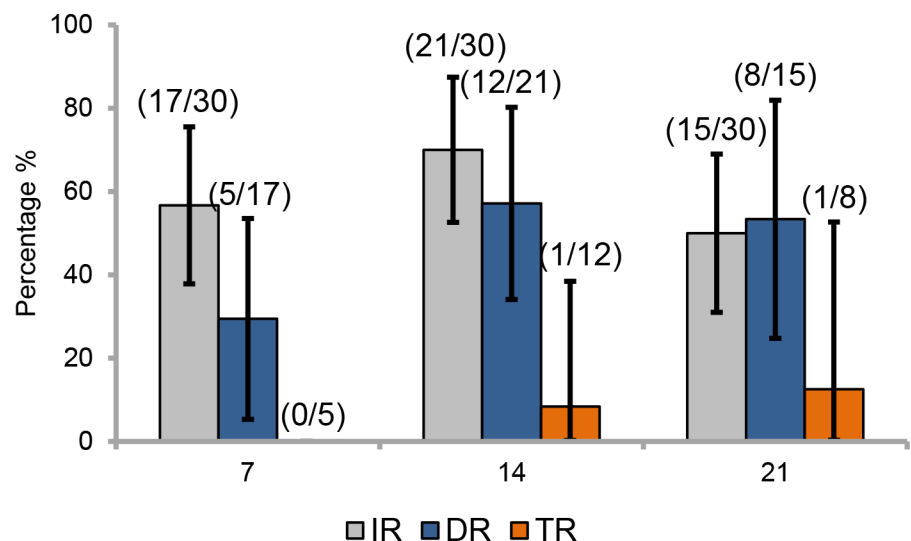


Fig 1. Infection, dissemination and transmission rates of *Aedes aegypti* guadeloupe to YFV (IEC-4408, 1E lineage). Mosquitoes were exposed to an infectious blood meal with YFV provided at a titer of $10^{6.5}$ ffu/mL. After infection, mosquitoes were examined at 7, 14, and 21 days post-infection. Error bars show the 95% confidence interval. In brackets, the number of mosquitoes examined. IR: the proportion of mosquitoes with infected body among engorged mosquitoes; DR: the proportion of mosquitoes with infected head among mosquitoes with infected body; TR: the proportion of mosquitoes with infectious saliva among mosquitoes with infected head.

<https://doi.org/10.1371/journal.pone.0204710.g001>

with infected body decreased to 50% (15/30) and among them, more than half (53.3%; 8/15) could ensure a viral dissemination. A slightly higher proportion of mosquitoes (12.5%; 1/8) with disseminated infection presented virus in saliva; one mosquito had 200 viral particles. Rates did not significantly vary according to dpi: 7 dpi (Chi-square test: $\chi^2 = 2.57$, $df = 2$, $p = 0.27$), 14 dpi (Chi-square test: $\chi^2 = 3.21$, $df = 2$, $p = 0.20$), and 21 dpi (Chi-square test: $\chi^2 = 0.65$, $df = 2$, $p = 0.72$).

Discussion

Except Trinidad and Tobago in 1979 [19], the Caribbean has not suffered from YF since 1960. The ongoing YFV circulation in Brazil raises concern regarding viral importation into the Caribbean. However, the requirement of YF vaccination is not mandatory in many Caribbean islands (e.g. Haiti, Cuba), but restricted to the travelers coming from YF-epidemic countries (http://www.who.int/ith/ITH_country_list.pdf?ua=1). The disease control relies only on the check of vaccination card, which is insufficient for YF prevention. Thus, YF is still a threat for this region where *Ae. aegypti* is widely distributed. Here, although not based on vertebrate animal transmission model, we demonstrated that *Ae. aegypti* from Guadeloupe are susceptible to YFV and able to transmit viral particles from 14 days post-infection.

Viral infection, dissemination and transmission increased along with dpi. Infection and dissemination reached a peak at 14 dpi (70% and 57% for IR and DR, respectively), suggesting that the midgut has a limited role as barrier to the viral dissemination in the mosquito general cavity. Transmission was only detected from 14 dpi suggesting an extrinsic incubation period (i.e. period between the ingestion of infectious blood meal and the excretion of virus in saliva) is between 7 and 14 days as shown for *Ae. aegypti* populations from Congo and Brazil [10]. However transmission was quite low (i.e. 8%) suggesting a significant role of salivary glands to retain viral particles. At 21 days post-infection, transmission was more efficient with 12% of mosquitoes presenting disseminated infection and delivering virus in saliva.

It is now widely admitted that vector competence depends on the virus genotype, the mosquito genotype and their interactions, promoting local adaptation of viral lineages to mosquito vector populations [20]. The table below (Table 1) presents the vector competence of several *Ae. aegypti* populations from Africa, America, Asia and South Pacific region to several lineages/genotypes of YFV, exemplifying the specific outcome to each combination virus-vector.

The pattern of *Ae. aegypti* Guadeloupe infected with a YFV belonging to the 1E lineage (IEC-4408; [10]) should be close to the profile of mosquitoes from the American continent. *Ae. aegypti* from Rio and Manaus presented similar IR, DR and TR when compared to *Ae. aegypti* Guadeloupe (see Table 1, [10]). It has been demonstrated previously that *Ae. aegypti* from the Caribbean were genetically close to mosquitoes from Brazil [27]. However, other factors should be considered to assess the risk of transmission; while YF is still absent from Asia, the vector competence of Asian *Ae. aegypti* (see Table 1; Phnom Penh: DR = 64%, Ho Chi Minh city: DR = 48%) was higher than values of *Ae. aegypti* from Africa. These factors include: vector densities, trophic preference of vectors for humans, proportion of immunologically naïve humans, and environmental conditions favorable to transmission. Surveillance of travelers coming from YFV-endemic regions of Africa or South America able to initiate a local transmission in the Caribbean should be reinforced. Likewise, vaccination coverage should be reexamined as the live-attenuated 17D is one of the most effective vaccines available against this arbovirus.

Table 1. Vector competence of different *Aedes aegypti* populations to YFV.

| Mosquitoes | | F ^a | Titer of blood meal | Virus strain | Day post-infection | IR ^b | DR ^c | TR ^d | Reference |
|--------------|-------------------|---------------------------------|--|-----------------------|--------------------|-------------------------|------------------------|----------------------|-----------|
| Country | Locality | | | | | | | | |
| Kenya | Nairobi | F1 | 6.7–7.5 Log ₁₀ pfu/mL | East African | 14 | 7 (5/75) | 0 (0/5) | ND | [21] |
| | Mariakani | F1 | 6.7–7.5 Log ₁₀ pfu /mL | East African | 14 | 41 (31/75) | 45 (14/31) | ND | |
| | Kerio Valley | F1 | 6.7–7.5 Log ₁₀ pfu /mL | East African | 14 | 11 (8/75) | 38 (3/8) | ND | |
| | Kakamega | F1 | 6.7–7.5 Log ₁₀ pfu /mL | East African | 14 | 25 (19/75) | 42 (8/19) | ND | |
| South Africa | Durban | F3 | >9.5 Log ₁₀ MID ₅₀ /mL | BA-55 (Nigeria, 1987) | 20 | ND | 15 (7/48) | ND | [22] |
| | | F2 | 7.9 Log ₁₀ MID ₅₀ /mL | BC7914 (Kenya) | 18–25 | ND | 2 (1/45) | ND | |
| | Skukusa | F2/3 | >9.5 Log ₁₀ MID ₅₀ /mL | BA-55 (Nigeria, 1987) | 20 | ND | 10 (4/38) | 0 (0/4) ^f | |
| | | F1 | 8 Log ₁₀ MID ₅₀ /mL | BC7914 (Kenya) | 15–20 | ND | 6 (2/32) | ND | |
| | Pafuri | F1 | 7.5 Log ₁₀ MID ₅₀ /mL | BA-55 (Nigeria, 1987) | 20 | ND | 0 (0/40) | ND | |
| | | F1 | 8 Log ₁₀ MID ₅₀ /mL | BC7914 (Kenya) | 15–25 | ND | 9 (4/46) | ND | |
| Guinea | Boulbinet | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 3 (4/123) | ND | [24] |
| Capo Verde | Praia | F1/2 | 10 ⁷ ffu/mL | S-79 (Senegal, 1979) | 14 | ND | 15 (6/41) | 50 (3/6) | [23] |
| Brazil | Rio | F1 | 10 ⁶ pfu/mL | 74018 (Brazil, 2001) | 21 | 45 (9/20) | 22 (2/9) | 50 (1/2) | [10] |
| | | F1 | 10 ⁶ pfu/mL | 4408 (Brazil, 2008) | 21 | 85 (17/20) | 59 (10/17) | 60 (6/10) | |
| | | F1 | 10 ⁶ pfu/mL | S-79 (Senegal, 1979) | 21 | 60 (12/20) | 75 (9/12) | 22 (2/9) | |
| | Goiania | F1 | 10 ⁶ pfu/mL | 74018 (Brazil, 2001) | 21 | 65 (13/20) | 92 (12/13) | 0 (0/12) | [24] |
| | | F1 | 10 ⁶ pfu/mL | 4408 (Brazil, 2008) | 21 | 10 (2/20) | 100 (2/2) | 50 (1/2) | |
| | | F1 | 10 ⁶ pfu/mL | S-79 (Senegal, 1979) | 21 | 0 (0/20) | ND | ND | |
| | Manaus | F1 | 10 ⁶ pfu/mL | 74018 (Brazil, 2001) | 21 | 55 (11/20) | 54 (6/11) | 33 (2/6) | [24] |
| | | F1 | 10 ⁶ pfu/mL | 4408 (Brazil, 2008) | 21 | 70 (14/20) | 85 (12/14) | 17 (2/12) | |
| | | F1 | 10 ⁶ pfu/mL | S-79 (Senegal, 1979) | 21 | 35 (7/20) | 14 (1/7) | 100 (1/1) | |
| | Milhas | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 0 (0/148) | ND | [24] |
| | Comendador Soares | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 1 (1/110) | ND | |
| | Quixeramobim | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 2 (2/120) | ND | |
| | Rocinha | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 3 (4/121) | ND | |
| | Tingua | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 5 (5/103) | ND | |
| | Pacuja | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 6 (4/71) | ND | |
| | Salvador | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 6 (7/111) | ND | |
| | Higienopolis | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 7 (8/120) | ND | |
| | Moqueta | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 8 (9/118) | ND | |
| | Feira de Santana | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 11 (5/47) | ND | |
| | Rio Branco | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 11 (13/117) | ND | |
| | Leandro Ferreira | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 12 (13/108) | ND | |
| | Cariacica | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 13 (15/119) | ND | |
| | Boa Vista | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 13 (15/116) | ND | |
| | Represa do Cigano | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 16 (9/56) | ND | |
| | Sao Luis | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 20 (22/112) | ND | |
| | Maringua | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 23 (27/119) | ND | |
| | Porto Velho | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 24 (29/119) | ND | |
| | Campo Grande | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 25 (26/104) | ND | |
| | Potim | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 27 (32/118) | ND | |
| | Belem | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 34 (37/109) | ND | |
| | Ananindeua | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 46 (52/112) | ND | |
| | Foz do Iguacu | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 49 (53/109) | ND | |
| Santos | F2 | 7–7.8 Log ₁₀ pfu /mL | 71528 MG2001 (Minas Gerais, 2001) | 10–14 | 35 (12/34) | 28 (11/39) ^e | ND | [25] | |
| | | 6.3 Log ₁₀ pfu /mL | 71528 MG2001 (Minas Gerais, 2001) | 21 | ND | 23 (5/22) | 20 (4/20) ^f | | |
| Venezuela | Maracay | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 14 (18/132) | ND | [24] |
| USA | West Palm Beach | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 25 (26/105) | ND | [24] |
| Cambodia | Phnom Penh | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 64 (67/104) | ND | [24] |
| Vietnam | Ho Chi Minh city | F1 | 10 ^{8.7} MID ₅₀ /mL | 74018 (Brazil, 2001) | 14 | ND | 48 (59/123) | ND | [24] |

(Continued)

Table 1. (Continued)

| Mosquitoes | | F ^a | Titer of blood meal | Virus strain | Day post-infection | IR ^b | DR ^c | TR ^d | Reference |
|------------|------------|----------------|--|---|--------------------|-------------------------|-------------------------|-------------------------|-----------|
| Country | Locality | | | | | | | | |
| Australia | Cairns | F2 | 10 ^{7.2} TCID ₅₀ /mL 10 ^{6.7} TCID ₅₀ /mL | BA-55 (Nigeria, 1987) OBS 7549 (Bolivia, 1999) | 14 | 80 (20/25) 24 (6/25) | 90 (18/20) 100 (6/6) | 72 (13/18) 100 (6/6) | [26] |
| | Townsville | F3 | 10 ^{7.2} TCID ₅₀ /mL 10 ^{6.7} TCID ₅₀ /mL | BA-55 (Nigeria, 1987) OBS 7549 (Bolivia, 1999) | 14 | 72 (18/25) 36 (9/25) | 83 (15/18) 89 (8/9) | 100 (15/15) 87 (7/8) | |
| Guadeloupe | Les Abimes | F1 | 10 ^{6.5} ffu/mL | 4408 (Brazil, 2008) | 14 | 70 (21/30) | 57 (12/21) | 8 (1/12) | Our study |
| | | | | | 21 | 50 (15/30) | 53 (8/15) | 12 (1/8) | |

^a Generation

^b Infection rate

^c Dissemination rate

^d Transmission rate

^e Dissemination efficiency

^f Transmission efficiency.

<https://doi.org/10.1371/journal.pone.0204710.t001>

Acknowledgments

We thank Laurence Mousson and Marie Vazeille for technical help, Cédric Ramdini and Joel Gustave for their support during mosquito sampling campaigns, and Pedro Fernando da Costa Vasconcelos for providing the viral strain. P-S.Y. was supported by the Institut Pasteur and the National Health Research Institutes in Taiwan.

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Writing – review & editing: Anna-Bella Failloux.

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