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# Review Article: A Review of Mosquitoes Associated with Rift Valley Fever Virus in Madagascar

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*Abstract.* Rift Valley fever (RVF) is a viral zoonotic disease occurring throughout Africa, the Arabian Peninsula, and Madagascar. The disease is caused by a *Phlebovirus* (RVF virus [RVFV]) transmitted to vertebrate hosts through the bite of infected mosquitoes. In Madagascar, the first RVFV circulation was reported in 1979 based on detection in mosquitoes but without epidemic episode. Subsequently, two outbreaks occurred: the first along the east coast and in the central highlands in 1990 and 1991 and the most recent along the northern and eastern coasts and in the central highlands in 2008 and 2009. Despite the presence of 24 mosquitoes species potentially associated with RVFV transmission in Madagascar, little associated entomological information is available. In this review, we list the RVFV vector, *Culex antennatus*, as well as other taxa as candidate vector species. We discuss risk factors from an entomological perspective for the re-emergence of RVF in Madagascar.

## INTRODUCTION

Rift Valley fever (RVF) is a disease of humans and domestic animals in several African countries.[1] The disease is caused by an arthropod-borne virus (RVF virus [RVFV]) belonging to the family *Bunyaviridae*, genus *Phlebovirus*, which was first isolated in 1931 during outbreak in Kenya.[2] RVF touches a wide range of wild and domestic vertebrate species, and the severity of the disease varies according to the age of the host.[3] A recent RVF outbreak that occurred in Madagascar was probably associated with infected domestic animals imported from east Africa.[4,5] Another study suggested that this outbreak most likely originated from an endemic cycle localized in southern Madagascar, where virus circulation may occur annually.[6] Although not quantified, it is possible that these two mechanisms co-occur in Madagascar, with a recurrent introduction that helps RVFV maintenance and recirculation in the endemic cycle.[7] The role of mosquitoes in RVF transmission on the island was considered to be associated with the first RVFV isolation and the 2008–2009 outbreak.[8,9]

Even given the presence of 32 mosquito species in Madagascar that are known or suspected vectors of RVFV, little information is available for these taxa from an entomological perspective. Herein, we focus on the mosquito species present in Madagascar associated with RVFV transmission based on data in the literature. Our objective here is to determine the status of each vector and review aspects of their biology, geographical distribution, and ecology that might be important for RVFV vector transmission.

## HISTORY OF RVF OCCURRENCE IN MADAGASCAR

Three RVFV circulation periods are known to have taken place in Madagascar. In 1979, the virus was isolated from mosquitoes captured in a humid forest near Andasibe-Périnet in central eastern Madagascar, but no evidence of an epizootic period was reported.[8] In 1990 and 1991, RVFV was isolated from humans and livestock in the lowland eastern coastal and upland central highlands, respectively.[10,11] Twenty years later, in 2008 and 2009, an RVF outbreak was reported in several regions of the island with virus detection and isolation in mosquitoes, humans, and livestock.[4,9] As supporting evidence, anti-RVFV (immunoglobulin M [IgM] and IgG) antibodies have been detected in livestock and humans during periods between virus outbreaks.[12,13] These results suggest a silent but continuous circulation of the virus in livestock.

## RVF TRANSMISSION

On a global basis, the occurrence and spread of the RVF outbreaks on the African mainland and the Arabia Peninsula are variable and found in different ecoclimatic zones; vector species and vector capacity are influenced by ecological,[14] behavioral,[15] and RVFV molecular factors.[16,17] For example, in an arid area, such as the Arabian Peninsula, RVFV transmission by mosquitoes is related to rainfall and water runoff management, with temporary rain pools and floodplains representing favorable vector breeding sites.[18–20] In subhumid areas in east Africa, RVF emergence is partly caused by the vertical transmission of the virus in eggs of *Aedes* spp., especially those belonging to the *Neomelaniconion* subgenus,[21] that are laid in wetland habitats. In the context of El Niño–Southern Oscillation (ENSO) events, wetlands become flooded after abnormally high rainfall, which in turn, favors the hatching of infected *Aedes* eggs and the development of the immature stages. This leads to the epizootic episode after adult emergence, which is soon followed by a parallel emergence of *Culex*.[22,23] In west Africa, the virus circulates in the Sahelian area transmitted by *Aedes* and *Culex* mosquitoes, which develop in temporary pools where cattle and sheep concentrate during the rainy season. Dam construction and ecological modification of the environment, including the presence of rice fields, may lead to the outbreaks directly associated with vector abundance.[24,25]

Mosquitoes can become infected by feeding on an infected host that exhibits a viremia higher than $10^{1.3}$ plaque-forming unit (pfu)/mL.[26] RVFV can be transmitted to vertebrates and mosquitoes by several mechanisms. (1) The transmission of RVFV occurs through direct contact with body fluids (blood, saliva, and/or nasal discharges) of infected animals or aborted ruminant fetuses.[27,28] Humans can be infected by contact with infected tissues or aerosols of infected blood generated during ruminant abortion or animal slaughter.[27,29] (2) Vector transmission occurs through the bite of infected mosquitoes.[30] The

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first evidence of vector transmission goes back to 1948, when RVFV was first isolated in a laboratory experiment and identified from field-collected mosquitoes (*Eretmapodites* spp. and *Ae.* [*Aedimorphus*] *tarsalis* group).[31] (3) Vertical transmission of RVFV from infected female mosquitoes to their progeny also occurs. This means of transmission was reported in the field for *Ae.* (*Neomelaniconion*) sp.[21] and suggested for *Ae.* (*Aedimorphus*) subgenus.[18]

Although RVF transmission to humans by infected mosquitoes was never been directly reported, probably more than one species of the *Ae. tarsalis* group and 78 mosquito species from eight genera have been associated with RVFV. Based on the functioning of virus–vector systems,[32] three criteria are necessary to show the vector status of a given mosquito species: (1) the isolation of RVFV from wild-caught mosquitoes, (2) the observation in a laboratory setting of vector competence, and (3) evidence from the field of an association between the arthropod vector and the vertebrate populations in which the infection is occurring. In this paper, we propose that mosquito vectors can be subdivided into three categories: vector, candidate vector, and potential vector. If only one criterion is validated, the mosquito species is qualified as a potential vector; in the case of two criteria, the mosquito species is qualified as a candidate vector, and for all three criteria, the mosquito species is qualified as a vector.

## MOSQUITO VECTORS IN MADAGASCAR

Twenty-four species have been associated with RVFV infections in Madagascar, representing 11% of known culicidian species on the island.[33] Most of these species have zoophilic behavior (cattle, sheep, and goat), and some of them are described opportunistic anthropophilic feeders.[15,34,35] These taxa belong to the genera *Aedes*, *Anopheles*, *Culex*, *Eretmapodites*, and *Mansonia* following traditional morphological classifications.[36,37]

In Madagascar, six species of *Aedes* fall into the vector, candidate vector, and potential vector categories associated with RVFV. Most of these are known to feed on animals, and *Ae. albopictus* and *Ae. aegypti* are highly anthropophilic.[12] These six taxa belong to subgenera known and/or suggested (based on fieldwork) to vertically transmit RVFV on the African mainland (*Aedimorphus*, *Neomelaniconion*, and *Stegomyia*), suggesting that RVFV maintenance by vertical transmission is possible in Madagascar. Five *Anopheles* species are associated or potentially associated with RVF transmission; all are zoophilic or zooanthropophilic taxa,[33] and three species are reported to be infected with RVFV in continental Africa and Madagascar.[9,21] Ten *Culex* vector species associated with RVF infection are present in Madagascar. Nine of them are already reported in the field to be RVFV-positive in Africa and Madagascar.[9,19,25,38–41] One *Eretmapodites* species and two *Mansonia* species also could be potential vectors in Madagascar.

Among these mosquito species, four were found naturally infected in Madagascar: *An. coustani*, *An. squamosus*, *Cx. antennatus*, and *Ma. uniformis*.[9,42] Recently considered as an RVFV candidate vector,[15] *Cx. antennatus* also has a high vector competence.[43] Only this species in Madagascar meets the three criteria needed to be considered an RVFV vector. Moreover, this zooantropophilic species is present and abundant in all five biogeographical domains of Madagascar. Recently considered as an RVFV candidate vector,[15] *Cx. antennatus* has high vector competence.[43] Consequently, the role of this species as a major vector of RVFV is confirmed. *An. coustani* and *An. squamosus* are the most abundant *Anopheles* taxa in Madagascar, both being zoophilic with broad distributions across the island.[12,15] Information is currently not available on the level of vector competence, and hence, both species remain RVFV candidate vectors.[15]

Using this proposed system of categorization, seven other zooanthropophilic species should be included: *Cx. univittatus*, *Cx. pipiens*, *Cx. quinquefasciatus*, *Cx. poicilipes*, *Cx. tritaeniorhynchus*, *Er. quinquevittatus*, and *Ma. uniformis*. These species are also abundant and present across Madagascar.[12] With information on natural and experimental infection of these *Culex* and *Eretmapodites* species (Table 1) and the absence of RVFV detection in the field in Madagascar, these species are considered as candidate vectors. No experimental information is available for *Ma. uniformis* in the transmission of RVFV. However, this species is abundant, and humans are considered to be its principal host in Madagascar[12] and on the African mainland.[35] The remaining mosquito species listed in Table 1 and present in Madagascar should be considered as potential vectors.

## RISK FACTORS ASSOCIATED WITH MOSQUITO POPULATIONS

Excluding factors associated with vertebrates (species, movement, density, susceptibility, and vaccination),[69] mosquito vectors are major components of RVF risk, which we refer to as the entomological risk. Classically, this entomological risk takes into account mosquito density, population dynamics, trophic behavior, longevity of each mosquito population in a given place, and vector competence of each species/population for a given virus strain, including vertical transmission. These variables are almost certainly influenced by climate (temperature and rainfall), biotic variables (breeding sites and presence of vertebrate hosts), and vector control as observed in Madagascar[15,69,70] and other countries.[71]

In Madagascar, the distributions of mosquitoes classified as RVFV vectors, potential vectors, and candidate vector are notably different and associated with biogeographical domains.[12] These differences might explain regional differences in RVFV prevalence and outbreaks.[4,6] RVF circulation and occurrences generally happen during the wet and warm season,[4] which correlates with the period of highest mosquito density.[9,15,12] This increase in mosquito vector density is caused by the creation and maintenance of different breeding sites.[72] Indeed, mosquitoes species already associated with RVFV in Madagascar colonize different types of larval breeding sites, with rice fields being a dominant habitat.[33,69]

In Madagascar, vector control is primarily targeted against mosquitoes transmitting malaria through the use of indoor residual spraying (IRS) and nets (insecticide-treated mosquito nets and long-lasting insecticidal mosquitoes nets).[73] No larvicidal measures have been undertaken on the island. The positive effect of these indoor treatments is to kill mosquitoes. Several RVFV vectors are exophilic species and probably escape these treatments. The negative effect is the appearance of more exophilic and zoophilic populations after indoor treatment, which was observed in Equatorial Guinea,[74] Tanzania,[75] Benin,[76] and Senegal.[77] For RVF infection, this negative effect is poorly documented and therefore, speculative. Consequently, vector control in Madagascar should not be a significant

TABLE 1
Mosquito species associated with RVF transmission around the world

| Genus and species* | Natural infection | | Infection | | Transmission | | References | | |
|---|---|---|---|---|---|---|---|---|---|
| | Country | Periods | ID | Rate (%) | ID | Rate (%) | NT | ID + IR | ID + TR |
| *Aedes* | | | | | | | | | |
| *Stegomyia* | | | | | | | | | |
| *africanus* | Uganda | 1956 | | | | | 44 | | |
| *Aedimorphus* | | | | | | | | | |
| *argenteopunctatus*† | | | | | 6.8, 7.8 $\log_{10}$ $CPD_{50}$/mL | 14, 80 | | | 45 |
| *cumminsii* | Senegal | 1983 | | | | | 21 | | |
| *dalzieli*† | Senegal | 1983 | | | | | 46 | | |
| *dentatus* | South Africa | 1969 | 6.8, 7.8 $\log_{10}$ $CPD_{50}$ pfu/mL | 90 | 6.8, 9.8 $\log_{10}$ $CPD_{50}$/mL | 32, 50 | 47 | 45 | 45 |
| *tarsalis* | Uganda‡ | 1948 | | | | | 31 | | |
| *vexans* | Saudi Arabia | 2000 | $10^{8.5}$ pfu/mL, $10^{10.1,10.2}$ pfu/mL | 8, 100 | $10^{10.1,10.2}$, $10^{8.5,8.6}$ pfu/mL | 23, 25 | 19 | 29, 48 | 48 |
| *ochraceus* | Senegal, Kenya | 1993, 2006 | | | | | 41, 49 | | |
| *fowleri*† | | | $10^{1.3,1.6}$ pfu/mL, > $10^{6.4}$ pfu/mL | 11, 89 | $10^{5.4}$ pfu/mL | 43 | | 26 | 26 |
| *Finlaya* | | | | | | | | | |
| *notoscriptus* | | | $10^{7}$ pfu/mL | 86 | | | | 50 | |
| *japonicus* | | | ≥ $10^{8.5}$ pfu/mL | > 90 | | | | 51 | |
| *Neomelaniconion* | | | | | | | | | |
| *circumluteolus*† | Uganda, South Africa | 1955 | ≥ $10^{8}$ pfu/mL | 76 | ≥ $10^{8}$ pfu/mL | 21 | 44 | 52 | 52 |
| *mcintoshi* | Zimbabwe, South Africa | 1969, 1974, 1978 | $10^{8}$ pfu/mL | 50 | ≥ $10^{8}$ pfu/mL | 14 | 53 | 52 | 52 |
| *palpalis* | Central African Republic | 1969 | ≥ $10^{8}$ pfu/mL | 86 | ≥ $10^{8}$ pfu/mL | 55 | 54 | 52 | 52 |
| *unidentatus* | | | 6.8, 7.8 $\log_{10}$ $CPD_{50}$ pfu/mL | 86 | 6.8, 9.8 $\log_{10}$ $CPD_{50}$/mL | 58 | | 45 | 45 |
| *Stegomyia* | | | | | | | | | |
| *africanus* | Uganda | 1956 | | | | | 44 | | |
| *dendrophilus* | Uganda | 1948 | | | | | 31 | | |
| *albopictus*† | | | 4.3, 5.9 $\log_{10}$ pfu/mL | 3, 89 | 4.7, 5.9 $\log_{10}$ pfu/mL | 4, 12 | | 55 | 55 |
| *aegypti*† | Sudan | 2007 | 5.8 $\log_{10}$ pfu/mL, ≥ $10^{8.0}$ pfu/mL | 70, 84 | 5.8 $\log_{10}$ pfu/mL, > $10^{8.9}$ pfu/mL | 7, 14 | 56 | 52, 57 | 52, 57 |
| *calceatus* | | | ≥ $10^{8}$ pfu/mL | 100 | ≥ $10^{8.9}$ pfu/mL | < 2 | | 52 | 52 |
| *Ochlerotatus* | | | | | | | | | |
| *atlanticus* | | | $10^{8.3}$, > $10^{9.5}$ pfu/mL | 63, 94 | $10^{8.3}$, > $10^{9.5}$ pfu/mL | 9, 40 | | 58 | 58 |
| *canadensis* | | | $10^{6.2,7.2}$ pfu/mL | 96 | $10^{6.2,7.2}$ pfu/mL | 10, 54 | | 59 | 59 |
| *cantator* | | | $10^{6.7}$ pfu/mL | 85 | $10^{6.2,7.2}$ pfu/mL | 3 | | 59 | 59 |
| *caspius* | | | ≥ $10^{5.3}$ pfu/mL | 100 | > $10^{7}$ pfu/mL | 20 | | 30 | 30 |
| *communis* | | | $10^{7.9}$, $10^{9.4}$ pfu/mL | 60 | NT | NT | | 60 | 60 |
| *detritus* | | | $10^{8.5}$ pfu/mL | 13 | | | | 61 | |
| *dorsalis* | | | $10^{7.3,8.8}$, $10^{7.9,9.4}$ pfu/mL | 57, 100 | $10^{7.3,9.4}$ pfu/mL | 0 | | 60, 62 | 60, 62 |
| *excrucians* | | | $10^{6.2,7.2}$ pfu/mL | 72 | $10^{6.2,7.2}$ pfu/mL | 11 | | 59 | 59 |
| *fitchii* | | | $10^{7.9}$, $10^{9.4}$ pfu/mL | 33 | $10^{7.3,9.4}$ pfu/mL | 0 | | 60 | 60 |
| *implicatus* | | | $10^{7.9}$, $10^{9.4}$ pfu/mL | 100 | $10^{7.3,9.4}$ pfu/mL | 0 | | 60 | 60 |
| *infirmatus* | | | > $10^{7.6}$, > $10^{9.5}$ pfu/mL | 62, 100 | > $10^{7.6,9.5}$ pfu/mL | < 1, 4 | | 58 | 58 |
| *juppi* | South Africa | 1980 | 3.6, 8 $\log_{10}$ pfu/mL | 6, 67 | 7.8 $\log_{10}$ pfu/mL | 25 | 57 | 63, 57 | 57 |
| *sollicitans* | | | $10^{6.2,7.2}$ pfu/mL | 90 | $10^{6.2,7.2}$ pfu/mL | 17 | | 59 | 59 |
| *sticticus* | | | $10^{7.9}$, $10^{9.4}$ pfu/mL | 77 | $10^{7.9}$, $10^{9.4}$ pfu/mL | 8 | | 60 | 60 |
| *stimulans* | | | $10^{7.9}$, $10^{9.4}$ pfu/mL | 50 | $10^{7.9}$, $10^{9.4}$ pfu/mL | 0 | | 60 | 60 |
| *taeniorhynchus* | | | $10^{6.2,7.2}$ pfu/mL | 25, 85 | $10^{6.2,7.2}$ pfu/mL | 12 | | 48, 59 | 59 |
| *caballus* | South Africa | 1953 | 3.6, 7.8 $\log_{10}$ pfu/mL | 24, 60 | 3.6, 7.8 $\log_{10}$ pfu/mL | 0 | 64 | 57 | 57 |
| *vigilax* | | | $10^{7}$ pfu/mL | 38 | | | | 50 | |
| *Protomacleaya* | | | | | | | | | |
| *triseriatus* | | | $10^{6.2,7.2}$ pfu/mL | 83 | $10^{6.2,7.2}$ pfu/mL | 36 | | 59 | 59 |

*(continued)*

TABLE 1
Continued

| Genus and species* | Natural infection | | Infection | | Transmission | | References | | |
|---|---|---|---|---|---|---|---|---|---|
| | Country | Periods | ID | Rate (%) | ID | Rate (%) | NT | ID + IR | ID + TR |
| *Skusea* | | | | | | | | | |
| *pembaensis* | Kenya | 2006 | | | | | 41 | | |
| *Anopheles* | | | | | | | | | |
| *Anopheles* | | | | | | | | | |
| *tenebrosus*†§ | | | NT | NT | NT | NT | | 30 | 30 |
| *coustani*† | Zimbabwe, Madagascar | 1969, 2008 | | | | | 9, 47 | | |
| *coustani* + *fuscicolor*† | Madagascar | 1979 | | | | | 8 | | |
| *crucians* | | | $10^{7.6}$, > $10^{9.5}$ pfu/mL | 48, 100 | $10^{7.6}$ pfu/mL, $10^{9.5}$ pfu/mL | < 1 | | 58 | 58 |
| *quadrimaculatus*† | | | > $10^{8.8}$ pfu/mL | 64 | ≥ $10^{8.8}$ pfu/mL | < 1 | | 62 | 62 |
| *Cellia* | | | | | | | | | |
| *squamosus*† | Kenya, Madagascar | 2006–2007, 2008 | | | | | 9, 41 | | |
| *pharoensis*† | Kenya | 1985 | ≥ $10^{6.0}$ pfu/mL | 100 | 9.5 $\log_{10}$ $SMICLD_{50}$/mL | 4† | 21 | 30 | 43 |
| *arabiensis*† | Sudan | 2007 | | 2 | | | 56 | 29 | |
| *multicolor* | | | 9.5 $\log_{10}$ $SMICLD_{50}$/mL | 90 | 9.5 $\log_{10}$ $SMICLD_{50}$/mL | 13 | | 43 | 43 |
| *stephensi*¶ | | | NT | NT | NT | NT | | 65 | 65 |
| *pauliani* + *squamosus*† | Madagascar | 1979 | | | | | 8 | | |
| *Myzomyia* | | | | | | | | | |
| *cinereus* | South Africa | 1974–1975 | | | | | 57 | | |
| *Coquillettidia* | | | | | | | | | |
| *fuscopennata* | Uganda | 1960 | | | | | 66 | | |
| *perturbans* | | | $10^{6.6}$, > $10^{9.5}$ pfu/mL | 47, 100 | $10^{6.6}$, $10^{9.5}$ pfu/mL | 17, 71 | | 58 | 58, 60 |
| *grandidieri* + *Ma. uniform*† | Madagascar | 1979 | | | | | 8 | | |
| *Culex* | | | | | | | | | |
| *Culex* | | | | | | | | | |
| *antennatus*† | Madagascar | 2008 | $10^{5.3,6}$ pfu/mL | 60, 100 | > $10^{7}$ pfu/mL, ≥ $10^{8}$ pfu/mL | 7, 84 | 9 | 30, 52 | 30, 52 |
| *annulirostris* | | | $10^{7}$ pfu/mL | 55 | | | | 50 | |
| *erythrothorax* | | | $10^{8.8}$ pfu/mL | 70 | ≥ $10^{8.8}$ pfu/mL | 7 | | 62 | 62 |
| *pipiens*† | Egypt, Kenya | 1977, 1987, 1991 | $10^{6.5}$ $MICLD_{50}$/mL, ≥ $10^{8}$ pfu/mL | 40, 91 | > $10^{7}$ pfu/mL, ≥ $10^{8}$ pfu/mL | 7, 100 | 39, 67 | 52, 68 | 30, 52 |
| *univittatus*† | Kenya | 2006 | 5.1, 6.5 $\log_{10}$ pfu/mL | 20, 87 | 5.1, 6.5 $\log_{10}$ pfu/mL | 33 | 41 | 57 | 57 |
| *quinquefasciatus*† | Kenya | 2006 | 4.6 $\log_{10}$ pfu/mL, $10^{7}$ pfu/mL | 25, 30 | ≥ $10^{8}$ pfu/mL to 4.6 $\log_{10}$ pfu/mL | 5, 44 | 41 | 50, 57 | 52, 57 |
| *bitaeniorhynchms*† | Kenya | 2006 | | | | | 41 | | |
| *tritaeniorhynchms*† | Saudi Arabia | 2000 | 6.9 $\log_{10}$ pfu/mL | 73 | | | 19 | 19 | |
| *tarsalis* | | | $10^{7.9}$, ≥ $10^{8.8}$ pfu/mL | 88, 93 | $10^{7.9}$, ≥ $10^{8.8}$ pfu/mL | 6, 31 | | 60, 62 | 60, 62 |
| *zombaensis* | South Africa, Kenya | 1981, 1989 | 5.2, 8 $\log_{10}$ pfu/mL | 35, 92 | | | 40, 67 | 40 | |
| *simpsoni* + *vansomereni* + *univittatus*† | Madagascar | 1979 | | | | | 8 | | |
| *antennatus* + *simpsoni* + *vansomereni*† | Madagascar | 1979 | | | | | 8 | | |
| *simpsoni* + *vansomereni* + *annulioris*† | Madagascar | 1979 | | | | | 8 | | |
| *neavei*† | South Africa | 1981 | 6.6, 8.5 $\log_{10}$ pfu/mL | 14 | | | 40 | 63 | |
| *salinarius* | | | $10^{6.2,7.2}$ pfu/mL | 51, 88 | $10^{6.2,7.2}$ pfu/mL | 1, 51, 11, 11 | | 59, 48 | 59 |
| *theileri*† | South Africa | 1971 | 5.3, 8 $\log_{10}$ pfu/mL | 68, 99 | 5.3, 6.4 $\log_{10}$ pfu/mL | 13, 70 | 47 | 57 | 57 |
| *nigripalpus* | | | ≥ $10^{8.8}$ pfu/mL | 49 | ≥ $10^{8.8}$ pfu/mL | 4 | | 62 | 62 |
| *perexiguus* | | | $10^{5.3,\geq 7}$ pfu/mL | 30, > 75 | > $10^{7}$ pfu/mL | 11 | | 30 | 30 |
| *restuans* | | | $10^{1.3}$ pfu/mL | 100 | $10^{1.3}$ pfu/mosquitoes | 40 | | 60, 62 | 60 |

*(continued)*

TABLE 1
Continued

| Genus and species* | Natural infection | | Infection | | Transmission | | References | | |
|---|---|---|---|---|---|---|---|---|---|
| | Country | Periods | ID | Rate (%) | ID | Rate (%) | NT | ID + IR | ID + TR |
| *Eumalanomyia* | | | | | | | | | |
| *rubinotus*† | | | 6.9 $\log_{10}$ pfu/mL | 32 | 6.9 $\log_{10}$ pfu/mL | 0 | | 57 | 57 |
| *Melanoconion* | | | | | | | | | |
| *erratiats* | | | $10^{7.3}$, 1010.1,10.2 pfu/mL | 9, 79 | $10^{10.1,\ 10.2}$ pfu/mL | 33 | | 48, 62 | 48 |
| *Neoculex* | | | | | | | | | |
| *territam* | | | $10^{6.2,7.2}$ pfu/mL | 74 | $10^{6.2,7.2}$ pfu/mL | 25 | | 59 | 59 |
| *Oculeomyia* | | | | | | | | | |
| *poicilipes*† | Senegal, Mauritania, Kenya | 1998, 1998–1999, 2006 | 7.8 $\log_{10}$ $CPD_{50}$ pfu/mL | 90 | 6.8, 9.8 $\log_{10}$ $CPD_{50}$/mL | 15, 80 | 25, 41 | 45 | 45 |
| *Culiseta* | | | | | | | | | |
| *inornata* | | | $10^{7.9}$, $10^{9.4}$ pfu/mL | 100 | $10^{7.3,9.4}$ pfu/mL | NT | | 60 | 60 |
| *minnesotae* | | | $10^{1.3}$ pfu/mL | 67 | $10^{1.3}$ pfu/mosquitoes | 0 | | 60 | 60 |
| *Eretmapodites* | | | | | | | | | |
| *sp.* | Uganda | 1948 | | | | | 31 | | |
| *quinquevittatus*† | South Africa | 1971 | 8.2, 7.2 $\log_{10}$ pfu/mL | 74, 81 | 8.2 $\log_{10}$ | > 30 | 47 | 57 | 57 |
| *Mansonia* | | | | | | | | | |
| *Mansonoides* | | | | | | | | | |
| *africana*† | Uganda, Kenya | 1959, 2007 | | | | | 41, 66 | | |
| *dyari* | | | $10^{5.7}$, $10^{7.6}$ pfu/mL | 33, 62 | $10^{5.7}$, $10^{7.7}$ pfu/mL | < 1, 9 | | 58 | 58 |
| *uniformis*† | Madagascar, Kenya | 1979, 2006 | | | | | 8, 41 | | |
| *Psorophora* | | | | | | | | | |
| *Psorophora* | | | | | | | | | |
| *ferox* | | | $10^{8.3}$, > $10^{9.5}$ pfu/mL | 90, 100 | $10^{8.3}$, > $10^{9.5}$ pfu/mL | 16, 40 | | 58 | 58 |

$CPD_{50}$ = cytopathic dose 50; ID = infection dose (the dose of virus to which the mosquito was exposed); IR = infection rate; NT = the oral experiment was not tested (i.e., mosquitoes were inoculated intrathoracically with RVFV); $MICLD_{50}$ = median mouse intracerebral lethal doses; $SMICLD_{50}$ = suckling mouse intracerebral 50% lethal doses; TR = percentage of refeeding mosquitoes that transmitted virus by bite.

* Nomenclature from the Walter Reed Biosystematics Unit at the Smithsonian Institution (wrbu.si.edu).

† Vector, candidate vector, and potential vector in Madagascar.

‡ The species found to be naturally RVFV-positive by Smithburn and others[31] was not specified, and it consisted of the *Ae. tarsalis* group.

§ Transmission obtained after inoculation of the virus in adult and/or larval stage.[30,65]

¶ Transmission obtained after inoculation of the virus in adult and/or larval stage.[30,65] Infection rate and transmission rate are obtained at 26 °C as mentioned in all studies.

component of variation of transmission risk of RVF. However, the appearance of more exophilic and zoophilic populations cannot be removed from the RVFV transmission risk factors list, because transmission involves mainly exophilic and zoophilic species.[33]

Vector competence of Malagasy mosquitoes, including their ability to transmit RVFV to their progeny, is very poorly known. Vertical transmission has been observed in Africa in the *Neomelaniconion* subgenera of the *Aedes* genus, which is also present in Madagascar, and hence, it may occur on the island.[12] Because of the lack of evidence in Madagascar of natural populations of *Aedes* spp. being infected with RVF, the role of vertical transmission in maintenance of the disease remains hypothetical. However, the majority of involved *Aedes* subgenera is present in Madagascar.[9,12,78] Additional detection of RVF is needed (especially in the western domain, where high RVFV prevalence has been reported, and the southwestern domain, where endemic foci areas have been suggested to occur[6]), particularly in the context of viral maintenance through a possible vertical transmission. Field studies on vector biology and RVF entomological surveys need to be further advanced to determine if endemic cycles occur.

## IS IT POSSIBLE TO IDENTIFY RVF RISK AREAS IN MADAGASCAR?

Recent history of RVFV circulation in Madagascar showed 13 administrative regions of the island, specifically the northern, eastern, and central domains, where RVF epidemics/epizootics occurred.[4] The highest RVFV prevalence rates were observed in livestock in the western and northern domains.[6] The suggested RVFV candidates vectors (*An. squamosus* and *An. coustani*) and major vector (*Cx. antennatus*) reproduce in areas with large areas of water.[33] Consequently, remote sensing technology can be relevant to predict RVF outbreaks by identifying the environmental factors, such as breeding sites and rainfall, associated with the abundance of RVF vectors that have been observed on mainland Africa.[1,79,80] In Madagascar, this technique was used on a local scale of one domain during a malaria study[81] and could provide interesting insights associated with RVF entomological surveys, particularly in the southwestern domain, where RVF is considered to be endemic.[6] Variation in monthly and annual precipitations (http://iridl.ldeo.columbia.edu/) and patterns of variation in larval development are important factors that vary between biogeographical domains[69]; hence, this technology should be used for the identification RVF risk areas. It could be very useful to estimate the relationship between abundance of breeding sites and density of adult vectors for additional vector surveillance and control.

## GENERAL CONCLUSIONS

In Madagascar, there are 23 mosquito species considered as vectors or potential vectors of RVFV. Only one species, *Cx. antennatus*, meets the three criteria for classification as an RVFV vector and should be considered as an important vector of this disease. Several other species, such as *An. squamosus*, *An. coustani*, *Cx. univittatus*, *Cx. pipiens*, and *Ma. uniformis*, should be classified as candidate vector species. To date, contrary to what has been observed in different parts of Africa, no Malagasy *Aedes* species has been involved in the transmission of this fever. However, several species, including endemics, belonging to the *Aedes* subgenera involved in transmission and maintenance of RVFV in Africa, specifically *Neomelaniconion* and *Aedimorphus*, occur in Madagascar. Finally, a considerable amount of information and data is lacking for understanding of RVF transmission on the island, and the vector component is one of the key factors for deciphering past outbreaks and if possible, predicting future events.

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## REFERENCES

1. Peters CJ, Linthicum KJ, 1994. Rift Valley fever. Beran GW, ed. *CRC Handbook Series in Zoonoses. Section B: Viral Zoonoses*, 2nd Ed. Boca Raton, FL: CRC Press Inc., 125–138.
2. Daubney R, Hudson JR, Garnham PC, 1931. Enzootic hepatitis or Rift Valley fever: an undescribed virus disease of sheep, cattle and man from East Africa. *J Pathol Bacteriol 34:* 545–579.
3. Lefevre PC, 1997. Actualité de la fièvre de la Vallée du Rift: quels enseignements tirer des épidémies de 1977 et 1987? *Rev Med Trop Parasitol Bacteriol Clin Lab 57:* 61–64.
4. Andriamandimby SF, Randrianarivo-Solofoniaina AE, Jeanmaire EM, Ravololomanana L, Razafimanantsoa LT, Rakotojoelinandrasana T, Razainirina J, Hoffmann J, Ravalohery JP, Rafisandratantsoa JT, Rollin PE, Reynes JM, 2010. Rift Valley fever during rainy seasons, Madagascar, 2008 and 2009. *Emerg Infect Dis 16:* 963–970.
5. Carroll SA, Reynes JM, Khristova ML, Andriamandimby SF, Rollin PE, Nichol ST, 2011. Genetic evidence for Rift Valley fever outbreaks in Madagascar resulting from virus introductions from the east African mainland rather than enzootic maintenance. *J Virol 85:* 6162–6167.
6. Jeanmaire E, Rabenarivahiny R, Biarmann M, Rabibisoa L, Ravaomanana F, Randriamparany T, Andriamandimby SF, Squarzoni Diaw C, Fenozara P, de La Rocque S, Reynes J-M, 2011. Prevalence of Rift Valley fever infection in ruminants in Madagascar after the 2008 outbreak. *Vector Borne Zoonotic Dis 11:* 395–402.
7. Favier C, Chalvet-Monfray K, Sabatier P, Lancelot R, Fontenille D, Dubois MA, 2006. Rift Valley fever in West Africa: the role of space in endemicity. *Trop Med Int Health 2:* 1878–1888.
8. Clerc Y, Coulanges P, 1979. Rapport du laboratoire d'arbovirus pour 1978. *Arch Inst Pasteur Madagascar 47:* 64–68.
9. Ratovonjato J, Olive MM, Tantely ML, Andrianaivolambo L, Tata E, Razainirina J, Jeanmaire EM, Reynes JM, Elissa N, 2010. Detection, isolation, and genetic characterisation of Rift Valley fever virus from *Anopheles* (*Anopheles*) *coustani, Anopheles* (*Anopheles*) *squamosus*, and *Culex* (*Culex*) *antennatus* of the haute Matsiatra region, Madagascar. *Vector Borne Zoonotic Dis 11:* 753–759.

10. Morvan J, Saluzzo JF, Fontenille D, Rollin PE, Coulanges P, 1991. Rift Valley fever on the east coast of Madagascar. *Res Virol 142:* 475–482.
11. Morvan J, Rollin PE, Laventure S, Rakotoarivony I, Roux J, 1992. Rift Valley fever epizootic in central highlands of Madagascar. *Res Virol 143:* 407–415.
12. Fontenille D, 1989. Arbovirus transmission cycles in Madagascar. *Arch Inst Pasteur Madagascar 55:* 1–317.
13. Zeller HG, Rakotoharinadrasana HT, Rakoto-Andrianarivelo M, 1998. La fièvre de la vallée du Rift à Madagascar: risques d'infection pour le personnel d'abattoir à Antananarivo. *Revue Elev Méd vét Pays trop 51:* 17–20.
14. Mondet B, Diaite A, Ndione JA, Fall AG, Chevalier V, Lancelot R, Ndiaye M, Ponçon N, 2005. Rainfall patterns and population dynamics of *Aedes* (*Aedimorphus*) *vexans* arabiensis, Patton 1905 (Diptera: Culicidae), a potential vector of Rift Valley fever virus in Senegal. *J Vector Ecol 30:* 102–106.
15. Tantely ML, Rakotoniaina JC, Andrianaivolambo L, Tata E, Razafindrasata F, Fontenille D, Elissa N, 2013. Biology of mosquitoes that are potential vectors of Rift Valley fever virus in different biotopes of the Central Highlands of Madagascar. *J Med Entomol 50:* 603–610.
16. Pepin M, Bouloy M, Bird BH, Kemp A, Paweska J, 2010. Rift Valley fever virus (Bunyaviridae: Phlebovirus): an update on pathogenesis, molecular epidemiology, vectors, diagnostics and prevention. *Vet Res 41:* 1–40.
17. Muller R, Saluzzo J, Lopez N, Dreier T, Turell M, Smith J, Bouloy M, 1995. Characterization of clone 13, a naturally attenuated avirulent isolate of Rift Valley fever virus, which is altered in the small segment. *Am J Trop Med Hyg 53:* 405–411.
18. Mondet B, Diaïté A, Fall AG, Chevalier V, 2005. Relations entre la pluviométrie et le risque de transmission virale par les moustiques: cas du virus de la Rift Valley fever (RVF) dans le Ferlo (Sénégal). *Env Risque Sante 4:* 125–129.
19. Jupp PG, Kemp A, Grobbelaar A, Leman P, Burt FJ, Alahmed AM, Al Mujalli D, Khamees A, Swanepoel R, 2002. The 2000 epidemic of Rift Valley fever in Saudi Arabia: mosquito vector studies. *Med Vet Entomol 16:* 245–252.
20. Elfadil AA, Hasab-Allah KA, Dafa-Allah OM, 2006. Factors associated with Rift Valley fever in south-west Saudi Arabia. *Rev Sci Tech 25:* 1137–1145.
21. Linthicum KJ, Davies FG, Kairo A, 1985. Rift Valley fever virus (family Bunyviridae, genus Phlebovirus). Isolations from diptera collected during an inter-epizootic period in Kenya. *J Hyg (Lond) 95:* 197–209.
22. Davies FG, 1975. Observation on the epidemiology of Rift Valley ferver in Kenya. *J Hyg (Lond) 75:* 219–230.
23. Linthicum KJ, Anyamba A, Tucker CJ, Kelley PW, Myers MF, Peters CJ, 1999. Climate and satellite indicators to forecast Rift Valley fever epidemics in Kenya. *Science 285:* 397–400.
24. Fontenille D, Traore-Lamizana M, Diallo M, Thonnon J, Digoutte JP, Zeller HG, 1998. New Vectors of Rift Valley fever in West Africa. *Emerg Infect Dis 4:* 289–293.
25. Diallo M, Lochouarn L, Ba K, Sall AA, Mireille M, Lang G, Christian M, 2000. First isolation of the Rift Valley Fever virus from *Culex poicilipes* (Diptera: Culicidae) in nature. *Am J Trop Med Hyg 62:* 702–704.
26. Turell M, Faran ME, Cornet M, Bailey C, 1988. Vector competence of senegalese *Aedes fowleri* (Diptera: Culicidae) for Rift Valley fever virus. *J Med Entomol 25:* 262–266.
27. Flick R, Bouloy M, 2005. Rift Valley Fever Virus. *Curr Mol Med 5:* 827–834.
28. Swanepoel R, Coetzer JAW, 1994. Rift Valley fever. Synonyms: Enzootic hepatitis, Slenkdalkoors (Afrik.). Coetzer JAW, Thomson GR, Tustin RC, eds. *Infectious Diseases of Livestock with Special Reference to Southern Africa*. Cape Town, South Africa: Oxford University Press.
29. Moutailler S, Krida G, Schaffner F, Vazeille M, Failloux A-B, 2008. Potential vectors of Rift Valley fever virus in the Mediterranean Region. *Vector Borne Zoonotic Dis 8:* 749–754.
30. Turell MJ, Presley SM, Gad AM, Cope SE, Dohm DJ, Morrill JC, Arthur RR, 1996. Vector competence of egyptian mosquitoes for Rift Valley fever virus. *Am J Trop Med Hyg 54:* 136–139.
31. Smithburn KC, Haddow AJ, Gillett JD, 1948. Rift Valley fever: isolation of the virus from wild mosquitoes. *Br J Exp Pathol 29:* 107–121.
32. Reeves IN, 1957. Arthropods as vectors and reservoirs of animal pathogenic viruses. Hallauer C, Meyer KF, eds. *Handbuich der Virusforschung, v. 4 (Supplementary v 3)*. Vienna, Austria: Springer Verlag, 177–202.
33. Tantely ML, 2013. Biologie des moustiques vecteurs potentiels du virus de la fièvre de la Vallée du Rift (FVR) à Madagascar. Thèse de Doctorat de 3ème Cycle, Université d'Antananarivo, Madagascar.
34. Hamon J, Sales S, Coz J, Ouedraogo CS, Dyemkouma A, Diallo B, 1964. Observations sur les préférences alimentaires des moustiques de la République de Haute-Volta. *Bull Soc Pathol Exot 57:* 1133–1150.
35. White G, 1969. Blood feeding habits of malaria vector mosquitos in the South Pare district of Tanzania ten years after cessation of a dieldrin residual spraying campaign. *East Afr Med J 48:* 120–134.
36. Walter Reed Biosystematics Unit, 2013. *New Mosquito Classification*. Available at: http://www.mosquitocatalog.org/files/pdfs/mq_ClassificationNew201309.pdf. Accessed September 2013.
37. Grjebine A, 1966. Insectes, diptères, culicidae, anophelinae. *Arch Inst Pasteur Madagascar 22:* 1–487.
38. McIntosh BM, Jupp PG, De Sousa J, 1972. Further isolation of arboviruses from mosquitoes collected in Tongaland, South Africa, 1960–1968. *J Med Entomol 2:* 155–159.
39. Hoogstraal H, Meegan JM, Khalil GM, Adham FK, 1979. The Rift Valley fever epizootic in Egypt 1977–78. Ecological and entomological studies. *Trans R Soc Trop Med Hyg 73:* 624–629.
40. McIntoshi BM, Jupp PG, Dos Santos I, Rowe AC, 1983. Field and laboratory evidence implcating *Culex zombaensis* and *Aedes circumluteolus* as vector of Rift Valley fever virus in coastal South Africa. *S Afr J Sci 79:* 61–64.
41. Sang R, Kioko E, Lutomiah J, Warigia M, Ochieng C, O'Guinn M, Lee JS, Koka H, Godsey M, Hoel D, Hanafi H, Miller B, Schnabel D, Breiman RF, Richardson J, 2010. Rift Valley fever virus epidemic in Kenya, 2006/2007: The entomologic investigations. *Am J Trop Med Hyg 83:* 28–37.
42. Clerc Y, Coulanges P, 1980. Rapport du service de virologie. *Arch Inst Pasteur Madagascar 48:* 65–68.
43. Gad AM, Hassan MM, Said SE, Moussa MI, Wood OL, 1986. Rift Valley fever virus transmission by different egyptian mosquito species. *Trans R Soc Trop Med Hyg 81:* 694–698.
44. Weinbren MP, Williams MC, Haddow AJ, 1957. A variant of Rift Valley fever virus. *S Afr Med J 31:* 951–957.
45. Jupp P, Cornel A, Turell M, Bailey C, Beaman J, 1988. Vector competence tests with Rift Valley fever virus and five south African species of mosquito. *Am Mosq Control Assoc 4:* 4–8.
46. Meegan JM, Digoutte JP, Peters CJ, Shope RE, 1983. Monoclonal antibodies identify Zinga virus as Rift Valley fever virus. *Lancet 1:* 641.
47. McIntosh BM, 1972. Rift Valley fever. 1. Vector studies in the field. *J S Afr Vet Med Assoc 43:* 391–395.
48. Turell M, Dohm DJ, Mores CN, Terracina L, Wallette DL, Hribar LJ, Pecor JE, Blow JA, 2008. Potential for North American mosquitoes to transmit Rift Valley fever virus. *J S Afr Vet Med Assoc 24:* 502–507.
49. Fontenille D, Traore-Lamizana M, Zeller H, Mondo M, Diallo M, Digoutte J, 1995. Short report: Rift Valley fever in western Africa: isolations from *Aedes* mosquitoes during an interepizootic period. *Am J Trop Med Hyg 52:* 403–404.
50. Turell M, Kay B, 1998. Susceptibility of selected strains of australian mosquitoes (Diptera: Culicidae) to Rift Valley fever virus. *J Med Entomol 35:* 132–135.
51. Turell M, Byrd B, Harrison B, 2013. Potential for populations of *Aedes j. japonicus* to transmit Rift Valley fever virus in the USA. *J Am Mosq Control Assoc 29:* 133–137.
52. Turell MJ, Linthicum KJ, Patrican LA, Davies FG, Kairo A, Bailey CL, 2008. Vector competence of selected african mosquito (Diptera: Culicidae) species for Rift Valley fever virus. *J Med Entomol 45:* 102–108.
53. McIntosh BM, Jupp PG, dos Santos I, 1978. Rift Valley fever. *Arthropod Born Virus Inf Exch 35:* 3–9.
54. Digoutte J, Cordellier R, Robin Y, Pajot FX, Geoffroy B, 1974. Zinga virus (Ar 1976), a new arbovirus isolated in Central Africa. *Ann Inst Pasteur (Paris) 125:* 107–118.
55. Turell M, Bailey C, Beaman J, 1988. Vector competence of a Houston, Texas strain of *Aedes albopictus* for Rift Valley fever virus. *J Am Mosq Control Assoc 4:* 94–96.

56. Seufi AM, Galal FH, 2010. Role of *Culex* and *Anopheles* mosquito species as potential vectors of rift valley fever virus in Sudan outbreak, 2007. *BMC Infect Dis 10:* 1–8.
57. McIntosh BM, Jupp PG, Dos Santos I, Barnard BJH, 1980. Vector studies on Rift Valley fever virus in South Africa. *S Afr Med J 58:* 127–132.
58. Turell M, Britch S, Aldridge R, Kline D, Boohene C, Linthicum K, 2013. Potential for mosquitoes (Diptera: Culicidae) from Florida to transmit Rift Valley fever virus. *J Med Entomol 50:* 1111–1117.
59. Gargan TP, Clarck GG, Dohm DJ, Turell MJ, 1988. Vector potential of selected north american mosquito species for Rift Valley fever virus. *Am J Trop Med Hyg 38:* 440–446.
60. Iranpour M, Turell M, Lindsay L, 2011. Potential for canadian mosquitoes to transmit Rift Valley fever virus. *J Am Mosq Control Assoc 27:* 363–369.
61. Bouloy M, Dufour B, André-Fontaine G, Albina E, Chevalier V, Dorchies P, Duvallet G, Failloux AB, Fontenille D, Pépin M, Tarantola A, Thiry E, Chiron J, Hattenberger AM, Vannier P, 2008. Report: risque de propagation de la fièvre de la vallée du Rift (FVR) dans l'Océan Indien (La Réunion et Mayotte). *Agence Française de Sécurité Sanitaire et Alimentaire, Maisons-Alfort, France*. 1–124.
62. Turell M, Wilson W, Bennett K, 2010. Potential for north american mosquitoes (Diptera: Culicidae) to transmit Rift Valley fever virus. *J Med Entomol 47:* 884–889.
63. McIntosh BM, Jupp PG, 1981. Epidemiological aspects of Rift Valley fever in South Africa with reference to vectors. *Contrib Epidemiol Biostat 3:* 92–99.
64. Gear JHS, De Meillon B, Le Roux AF, Kofsky R, Innes RR, Steyn JJ, Oliff WD, Schulz KH, 1955. Rift Valley fever in South Africa; a study of the 1953 outbreak in the Orange Free State, with reference to the vector and the possible reservoir hosts. *S Afr Med J 29:* 514–518.
65. Turell MJ, Romoser WS, 1994. Effect of the developmental stage at infection on the ability of adult *Anopheles stephensi* to transmit Rift Valley fever virus. *Am J Trop Med Hyg 50:* 448–451.
66. Williams MC, Woodall JP, Corbet PS, Haddow AJ, 1960. An outbreak of Rift Valley fever occurring near Entebbe: entomological studies and further. *E Afr Vir Res Inst Rep 10:* 24–25.
67. Logan TM, Linthicum KJ, Davies FG, Binepal YS, Roberts CR, 1991. Isolation of Rift Valley Fever virus from mosquitoes (Diptera: Culicidae) collected during an outbreak in domestic animals in Kenya. *J Med Entomol 28:* 293–295.
68. Meegan JM, Khalil GM, Hoogstraal H, Adham FK, 1980. Experimental transmission and field isolation studies implicating *Culex pipiens* as a vector of Rift Valley fever virus in Egypt. *Am J Trop Med Hyg 29:* 1405–1410.
69. Nicolas G, Chevalier V, Tantely LM, Fontenille D, Durand B, 2014. A spatially explicit metapopulation model and cattle trade analysis suggests key determinants for the recurrent circulation of Rift Valley fever virus in a pilot area of Madagascar highlands. *PLoS Negl Trop Dis 8:* e3346.
70. Fontenille D, Campbell GH, 1992. Is *Anopheles mascarensis* a new malaria vector in Madagascar? *Am J Trop Med Hyg 46:* 28–30.
71. Robert V, Rocamora G, Julienne S, Goodman SM, 2011. Why are anopheline mosquitoes not present in the Seychelles? *Malar J 10:* 1–11.
72. Ndione JA, Diop M, Lacaux J-P, Gaye AT, 2008. Variabilité intra-saisonnière de la pluviometrie et émergence de la fièvre de la Vallée du Rift dans la vallée du fleuve Sénégal: nouvelles considérations. *Climatol 5:* 83–97.
73. Aregawi M, Cibulskis RE, Otten M, Williams R, 2009. *World Malaria Report, Global Malaria Programme. Surveillance Monitoring and Evaluation Unit*. Geneva: World Health Organization.
74. Reddy MR, Overgaard HJ, Abaga S, Reddy VP, Caccone A, Kiszewski AE, Slotman MA, 2011. Outdoor host seeking behaviour of *Anopheles gambiae* mosquitoes following initiation of malaria vector control on Bioko Island, Equatorial Guinea. *Malar J 10:* 1–10.
75. Russell TL, Govella NJ, Azizi S, Drakeley CJ, Kachur SP, Killeen GF, 2011. Increased proportions of outdoor feeding among residual malaria vector populations following increased use of insecticide-treated nets in rural Tanzania. *Malar J 10:* 1–10.
76. Moiroux N, Gomez MB, Pennetier C, Elanga E, Djènontin A, Chandre F, Djègbé I, Guis H, Corbel V, 2012. Changes in *Anopheles funestus* biting behavior following universal coverage of long-lasting insecticidal nets in Benin. *J Infect Dis 206:* 1622–1629.
77. Sougoufara S, Diédhiou SM, Doucouré S, Diagne N, Sembène PM, Harry M, Trape JF, Sokhna C, Ndiath MO, 2014. Biting by *Anopheles funestus* in broad daylight after use of long-lasting insecticidal nets: a new challenge to malaria elimination. *Malar J 13:* 2–7.
78. Clerc Y, Coulanges P, 1981. Rapport du laboratoire des arbovirus en 1980. *Arch Inst Pasteur Madagascar 49:* 65–68.
79. Ndione J-A, Lacaux J-P, Tourre Y, Vignolles C, Fontanaz D, Lafaye M, 2009. Mares temporaires et risques sanitaires au Ferlo: contribution de la télédétection pour l'étude de la fièvre de la vallée du Rift entre août 2003 et janvier 2004. *Sécheresse 20:* 153–160.
80. Soti V, Chevalier V, Maura J, Bégué A, Lelong C, Lancelot R, Thiongane Y, Tran A, 2013. Identifying landscape features associated with Rift Valley fever virus transmission, Ferlo region, Senegal, using very high spatial resolution satellite imagery. *Int J Health Geogr 12:* 1–11.
81. Rakotomanana F, Ratovonjato J, Randremanana RV, Randrianasolo L, Raherinjafy R, Rudant J-P, Richard V, 2010. Geographical and environmental approaches to urban malaria in Antananarivo (Madagascar). *BMC Infect Dis 10:* 1–11.