VECTOR-BORNE AND ZOONOTIC DISEASES
Volume 8, Number 1, 2008

DOI: 10.1089/vbz.2007.0649

Geographic Distribution and Developmental Sites of *Aedes albopictus* (Diptera: Culicidae) During a Chikungunya Epidemic Event

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ABSTRACT

***Aedes albopictus* is generally considered to have a low vectorial capacity because of its lack of host specificity. Nevertheless, it has been the sole vector of the Chikungunya virus in recent explosive epidemics on the islands of La Réunion and Mauritius. We report on investigations of the seasonal prevalence, container preferences, and geographic distribution of the species on La Réunion. *Ae. albopictus* showed strong ecological plasticity. In the warm wet season, small disposable containers were the principal urban breeding site, with 1939 positive containers in 750 houses. In the dry winter season, the species remained abundant throughout the island up to 800 m and was present to a maximum altitude of 1200 m. Natural containers were clearly important in this season, although productive sources were hard to find. The preferred natural developmental sites were bamboo stumps and rock holes, over 357 developmental sites observed in peri-urban and gully areas. Generalized logistic models indicated that the optimum sites contained clear water with high organic content and were situated in sites with moderate shade. Our data will provide input into the models of the epidemiology of the disease and design of vector control programs. Key words: *Aedes albopictus*—Arbovirus—Chikungunya epidemic—Geographical repartition—Larval ecology.**

INTRODUCTION

THE "ASIAN TIGER MOSQUITO," *Aedes* (*Stegomyia*) *albopictus* (Skuse) (Diptera: Culicidae), is native to Southeast Asia (Hawley 1988, Smith 1956) but has recently become established throughout the Americas and in at least nine countries in Europe, Africa, and the Middle East (Gratz 2004), disseminated by a worldwide commerce in used tires (Reiter 1998). Although capable of transmitting a large number of arboviruses (Mitchell 1995, Turrell 1988), the species has generally been considered as a "secondary" vector because it is not host specific. Nevertheless, it has been responsible for Chikungunya (CHIKV) transmission in recent explosive epidemics on the islands of La Réunion and Mauritius, where

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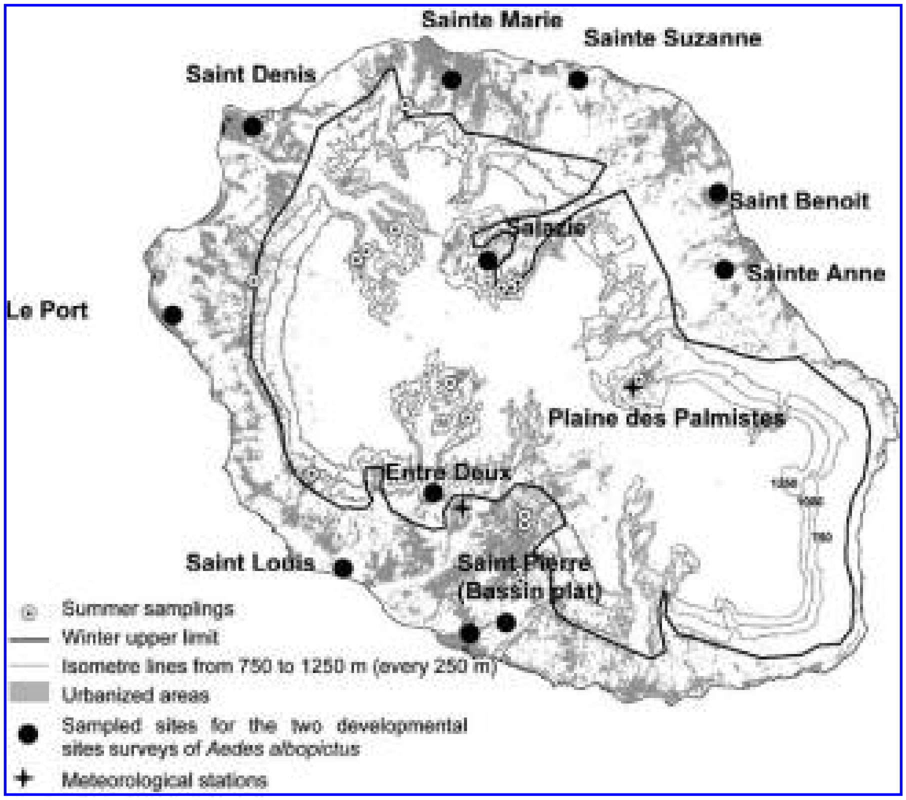

FIG. 1. Winter highest altitude limit of *Aedes albopictus* (star dots represent the highest points at which *Aedes albopictus* was found during the summer season). Black dots represent the sampled sites for the two *Ae. albopictus* breeding site surveys carried out during the summer and winter 2006.

the "classic" vector, *Aedes aegypti*, is virtually absent (Reiter et al. 2006, Schuffenecker et al. 2006). Based on clinical criteria it was estimated that 266,076 people contracted the disease in the period 2005–2006, with an attack rate of 35% (http://www.orsrun.net, 14 December 2006).

La Réunion is an island (2500 km^2) in the Indian Ocean, east of Madagascar. There are two distinct seasons: a cool and dry winter from May to October and a warmer, rainy summer from November to April. Among the 12 species of *Culicidae* that are present, *Ae. albopictus* was first recorded in 1913 (Edwards 1920). It was probably introduced several centuries before by trade with the Indian subcontinent. It is the dominant *Aedes* species, probably in part because of an effective mosquito-control campaign in the 1950s that reduced the *Ae. aegypti* populations to a few isolated rural sites (Hamon 1953, Reiter et al. 2006, Salvan and Mouchet 1994). *Aedes aegypti* was first described on the island of La Réunion in 1907, but no references to its abundance and distribution were made (Vassal 1907). Forty-six years later the distribution of this species was limited to a few sites on the west coast of the island, up to an elevation of 600 m (Hamon 1953). In 2001, Paupy et al. (2001) demonstrated marked structuration in *Ae. albopictus* populations, possibly associated with rainfall and other environmental factors. Other studies have suggested that winter and summer temperatures affect population biology and distribution (Alto and Juliano 2001).

Transmission of CHIKV began in 2005, continued through the dry austral winter, and resulted in a massive epidemic in 2006. Based on clinical criteria, it was estimated that the peak incidence in 2006 was observed in February, with more than 45,000 cases a week. There is no prior record of the virus on the island, and relatively little is known of the biology and behavior of the vector. We therefore conducted a

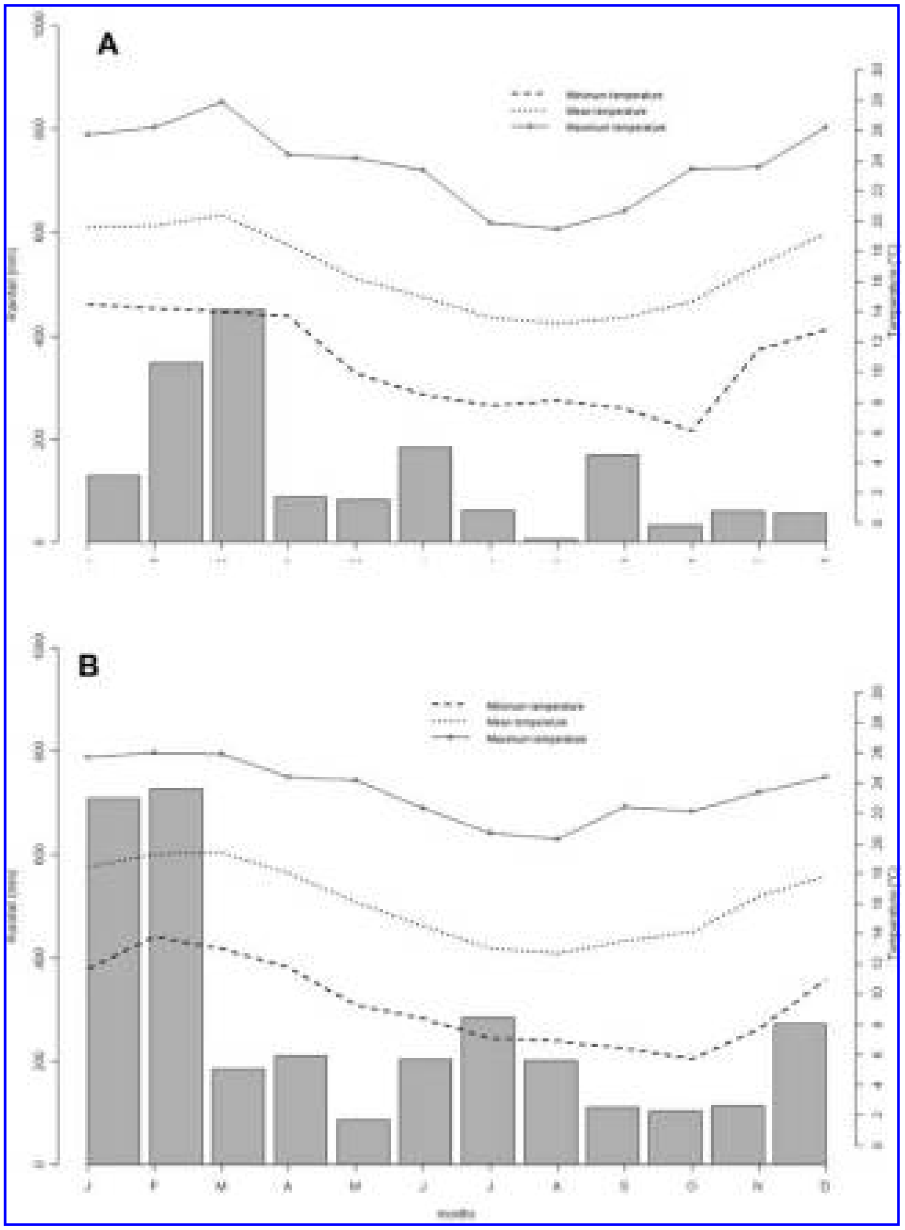

FIG. 2. Average rainfall, minimum, maximal, and average temperature data for two selected meteorological stations among 18 situated in the east (E) and in the west (W) of La Réunion (see Fig. 1), very close to the highest points at which *Aedes albopictus* was observed. **A**. Les Makes (900 m, west) **B.** Plaine des Palmistes (1025 m, east).

survey of the developmental sites and geographical repartition of *Ae. albopictus* during a CHIKV epidemic as a first step in understanding the dynamics of the epidemic.

MATERIALS AND METHODS

Mapping Ae. albopictus

To map the geographic distribution of *Ae. albopictus* on the island of La Réunion two entomological surveys were conducted in 2006, one during the rainy austral summer (January to June) and the other between 15 June and 15 August, during the dry winter. These surveys of adult and immature mosquitoes were conducted along roads located at the highest inhabited areas on the island in order to identify the upper elevation limit of *Ae. albopictus*. Only 12 species of Culicidae are present in La Réunion, and among them Ae. *albopictus* is the dominant *Aedes* species, so that adult and immature stages were easily recognizable. Following the road, the survey team would stop every 1 km, georeference the site with a GPS unit (Garmin), and inspect both sides of the road for a period of 5–10 minutes. Figure 1 shows the upper elevation limit of *Ae. albopictus*–positive sites in a geographical information system (GIS), source: BD-Topo IGN© (1997), UTM projection.

Meteorological data

Daily temperature and rainfall data were obtained from Meteo France and CIRAD weather stations. Figure 2 shows total temperature and rainfall by month for the two meteorological stations, Les Makes (900 m, west) and Plaine des Palmistes (1025 m, east), located closest to the highest elevations where *Ae. albopictus* was observed during the study.

Entomological surveys (immature stages)

Entomological developmental site surveys for *Ae. albopictus* were conducted in two phases. A first survey in urban areas was carried out in the following nine towns (human population of each town surveyed is included in parentheses): Saint Pierre (68,915), Saint Louis (43,519), Saint Benoit (31,560), Sainte Suzanne (18,144), Saint Denis (131,557), Saint André (43,174), Sainte Marie (26,582), le Port (38,412), Entre Deux (5170) (Fig. 1). In each town an attempt was made to carry a systematic sample of 100 households. However, because some households were closed or residents denied access to surveyors, a total of only 750 households were sampled in the nine towns. A second survey carried out in August 2006 covered two peri-urban areas located on the east coast (Saint Pierre, Bassin Plat) and west coast (Saint Benoit, Sainte Anne). The area sampled (total of 6.5 ha) included 200–300 m of gullies and the areas directly adjacent to roads. In this survey every container containing water was studied: first the depth of the water was measured, and then each container was emptied and the amount of water was measured. Next, larvae were collected with a pipette and brought back to the lab for identification of mosquitoes with a key elaborated from published works (Girod and Salvan 1998). The organic content of the water (low, medium, high), shade (no, yes), and the water quality (clear, tinted, polluted) were evaluated. If the larval habitat was shaded the whole day, the shade was scored as negative, and if the breeding site was exposed to sunshine at least once during the day, it was scored positively. This information was scored on separate forms, one for each developmental site.

All potential developmental sites with water were inspected for larvae and pupae of *Ae. albopictus* for both studies. All the houses inspected for both surveys had yards, even in urban areas; however, yards were bigger in peri-urban areas, and most of them were watered frequently.

Statistical analyses

An introductory Multiple Correspondence Analysis was conducted on the whole data set using the characteristic factors of the developmental sites to define which ones were the most discriminating. The characteristics studied were: clearness of water (clear, tinted, turbid), depth of the developmental site (small: 0.2–1.2 cm; medium: 1.5–6 cm; high: 6.5–100 cm), organic content rate (small, medium, high), type of developmental site (natural or artificial), and shade (yes, no). The developmental sites were divided into two groups on the first factorial plane (data not shown). These groups were formed by the factor "type of the developmental site." Therefore, it was decided to separate our data set into two subsets: "natural" and "artificial." Two independent models were built for each of the two variables (larvae and pupae presence and only pupae presence).

The two subsets were analyzed with generalized linear regression models with binomial distribution and logit link in R (version 2.3.1) (R Core Team, Vienna, Austria). Generalized logistic models (GLM) were used as the variable: *Ae. albopictus* was binary. The best model was determined with backward/forward stepwise procedure using Akaike's Information Criterion (AIC) (Burnham and Anderson, 1998). The coefficients were computed with the contrast "sum," which means that the coefficients of each factor sum to 0.

Moreover, for the ordered factors (i.e., clearness, depth, and organic content), quadratic and linear contrasts were integrated in the model. The quality of our fittings was assessed. We chose to measure the generalized coefficient of determination, R^2 of Cox and Snell (1989), to assess the predictive power of our models.

RESULTS

In the course of each of the different surveys conducted throughout the island (the two developmental site surveys and the two mapping surveys), no *Ae. aegypti* were found; only *Ae. Albopictus* were detected.

Mapping Ae. albopictus

In winter, *Ae. albopictus* was found up to 800 m all around La Réunion, with two exceptions: in the Circus of Salazie and Tampon, where its range reached 950 m and 1200 m, respectively. The lower altitudinal limits of *Ae. albopictus* observed in the less urbanized southeast region can be explained by the sampling method along roads located under 500 m in this part of La Réunion.

In summer, almost the same gradient of altitude (Fig. 1) was observed, except that the vector was found in the upper plateau situated in the center of La Réunion up to 1100 m, the southwest (1100 m), up to Plaines des Palmistes (1100 m for the high plateau of the east), the Circus of Cilaos (up to 1250 m), and the Circus of Mafate (from 750 to 1000 m).

Among the meteorological station data available, we chose to present only those from the two closest to the highest points where *Ae. albopictus* were found during the winter season (Fig. 2). There was more rainfall in the east, but lower temperatures were recorded in the west. The lowest minimum and average temperatures recorded where *Ae. albopictus* was present were 4°C and 12.6°C, respectively.

Developmental site surveys

The only *Aedes* species observed in any of the four surveys conducted in this study was *Ae. albopictus*; no *Ae. aegypti* specimens were collected.

During the summer survey, 750 houses were surveyed and 144 were positive, with a Breteau index of: 68.4 and a house index of 19.2%. In total, 2295 water collections were observed for the presence of immature mosquitoes, and only 703 were positive (31%) for both surveys (Tables 2 and 3).

The most abundant artificial developmental sites in urban areas during the summer survey were large wastes (48%), used tires (46%), and small containers (44%). In urban areas, the most abundant potential developmental sites (containers with water) were flower plates (1154 over 750 houses visited) and small wastes (296). As a whole in the summer urban survey, 27%

TABLE 1. *Aedes albopictus* DEVELOPMENTAL SITES ON NINE LOCALITIES OF LA RÉUNION (URBAN SITES) IN SUMMER.

Containers[a]	*No. positive/No. inspected*	*No. positive/Total no. of positive developmental sites*
Flower plates	226/1154 (20%)	226/513 (44%)
Small wastes (cans, plates, bags… 0–1.5 L)	99/296 (33%)	99/513 (19%)
Small containers (10–50 L)	80/183 (44%)	80/513 (16%)
Used tires	49/106 (46%)	49/513 (10%)
Flower pots	17/99 (17%)	17/513 (3%)
Large wastes (buckets, small plastic tanks, 1.5–10 L)	24/50 (48%)	24/513 (5%)
Large containers (50–100 L)	11/32 (34%)	11/513 (2%)
Gutters	0/2 (0%)	0/513 (0)
Car shelves	2/2 (100%)	2/513 (0.4%)
Others	5/15 (33%)	5/513 (1%)
Total	513/1939 (27%)	

[a]Large wastes included those containing between 1.5 L and 10 L. Small wastes included those containing less than 1.5 L. Large containers included those containing 50 L or more. Small containers included those containing between 10 L and 50 L.

Positive means that immature stages have been collected.

of the containers with water contained mosquitoes in immature stages (Table 1).

In the second survey, conducted in two peri-urban areas, the highest proportion of *Ae. albopictus* larvae- or pupae-positive artificial containers were barrels (70%) and used tires (60%), whereas flower plates (65%) and pots (42%) were the most observed larval development sites. The highest number of natural developmental sites encountered with larvae and pupae were bamboo stumps and rock holes (Table 2). Over all container types, the highest number of positive developmental sites found was for bamboo stumps, with 95% of the prospected flooded sites being positive. In the east part of La Réunion, the predominant natural developmental sites were bamboo stumps, mainly located along the river banks; this type of vegetation being mostly found in this part of the island. In the western part of La Réunion, gullies and the natural environment are dryer, and there is hardly any bamboo, the predominant natural developmental sites being rock holes. As a whole in the peri-urban/gully survey, 53% of the containers with water were positive for larvae and/or pupae. Overall containers, only 32% had pupae; among those, 18 had only pupae. The highest quantities of containers with only larvae were bamboo stumps (30) and rock holes (17). The presence of pupae was highly correlated with the larvae presence (0.97).

Models analysis: artificial developmental sites model (larvae and pupae presence)

As a whole, 237 observations with 96 *Ae. albopictus*-positive developmental sites (40.5%) were included in the analysis. With the contrasts "sum" for all the factors, the stepwise method with the best AIC value chose the additive model, without interactions between factors. All factors were significant for at least one modality (Table 3). The factor levels (small, medium, high) were significantly positively correlated with the presence of *Ae. albopictus* for the factors Organic content (–1.495, 0.398, 1.096) and Depth of the developmental site (–1.031, 0.160, 0.870). A significant negative correlation for the factor Clearness of water was observed (1.271, –0.370, –0.901), favoring the vector presence in clear waters and not favoring its presence in tinted and polluted waters. Shade had a strong significant negative influence on *Ae. albopictus* presence (–1.198). The quadratic effect was not significant for any of the three factors tested. The Generalized Coefficient of Determination (GCD) of the model was 0.39.

Natural developmental sites model (larvae and pupae presence)

In all, 119 observations with 94 positive developmental sites (79%) were included in the analysis. The complete additive model was kept so that it could be compared with the artificial developmental site model. A significant quadratic effect was observed for Depth, meaning that the effect of the "medium" level was stronger than that of the small and high levels (low: −1.136, medium: 0.791, high: 0.346). A significant (at $\alpha = 0.1$) linear effect of Organic content was also observed, with the medium content level (0.636) favoring the probability to observe *Ae. albopictus* (Table 3). Even if the modalities of the models were not all significant, they can be interpreted for the optimal conditions under which *Ae. Albopictus* would be observed. The value of the Wald test for the intercept denotes that the probability to observe *Ae. albopictus* was significantly higher than 0.5 in the studied sample. The GCD of the model was 0.11.

Pupae presence model

Pupae presence was analyzed on the whole data set, as no significant differences were observed between natural and artificial developmental sites. As a whole, 356 observations with 115 pupae-positive developmental sites (32%) were included in the analysis. The complete additive model was used. The factor levels were significantly positively correlated with the presence of pupae for the factors Organic content (−1.001, 0.316, 0.685) and Depth of the developmental site (−0.991, 0.414, 0.577). A significant negative correlation for the factor Clearness of water was observed (0.447, −0.325, −0.122). Shade had a significant negative influence on pupae presence (−0.402). The quadratic effect was only significant for the Depth factor;

TABLE 2. *Aedes albopictus* DEVELOPMENTAL SITES DETAILED TYPOLOGY ON TWO PERI-URBAN LOCALITIES OF LA RÉUNION (SAINT PIERRE AND SAINTE ANNE) IN WINTER

Containers	No. positive/No. inspected		Mean volume (L)	Min. volume (L)	Max. volume (L)	Mean depth (cm)	Min. depth (cm)	Max. depth (cm)	Shade
	L1-pupae	Pupae							
Natural		315 (20%)							
Leaf axilla	4/15 (27%)		0.061	0.007	0.3	5.633	1	10	10/12
Bamboo stumps	55/58 (95%)	24/58 (41%)	0.559	0.01	20	8.326	0.2	22	3/58
Palm leaves	1/5 (20%)	0/5 (0%)	0.052	0.001	0.15	1.2	0.5	3	1/5
Rock holes	33/39 (85%)	17/39 (44%)	2.122	0.01	56	4.526	0.5	34	25/39
Tree holes	1/2 (50%)	0/2 (0%)	0.05	0.05	0.05	2.75	0.5	5	0/2
Artificial		4/5 (80%)							
Basins	5/5 (100%)		5.14	1.7	10	8.8	3.5	13	4/5
Cans	9/15 (60%)	8/15 (53%)	1.584	0.02	6.5	5.6	0.5	18	7/15
Tin cans	5/8 (63%)	3/8 (38%)	0.264	0.002	1	3.625	0.5	17	4/8
Bottles	8/77 (10%)	6/77 (8%)	0.104	0.015	1.15	1.983	0.2	30	72/77
Lids	3/6 (50%)	2/6 (33%)	0.284	0.01	1.05	0.75	0.5	1.5	1/6
Small plastic wastes	8/20 (40%)		0.271	0.005	1.275	11.65	0.5	60	14/20
Barrels	7/10 (70%)	7/10 (70%)	85.875	0.5	200	53.5	4	100	4/10
Saucepans	1/7 (14%)	1/7 (14%)	1.236	0.15	4.25	5.286	0.5	13	3/7
Used tires	7/10 (70%)	6/10 (60%)	3.144	0.06	6.5	6.47	1	12	4/10
Pots	15/36 (42%)	13/36 (36%)	2.624	0.03	20	6.544	0.5	22	28/36
Buckets	4/6 (67%)	1/6 (17%)	5.724	0.053	20	12.833	1	23	3/6
Flower plates	24/37 (65%)	15/37 (41%)	0.294	0.005	1.25	1.881	0.4	9	21/37
Total	190/356 (53%)	115/356 (32%)							

TABLE 3. RESULTS OF THE LOGIT GLM MODELS (WALD TESTS) TESTING THE DIFFERENT FACTORS INFLUENCING THE PRESENCE OF *Ae. albopictus* IN ARTIFICIAL AND NATURAL DEVELOPMENTAL SITES

	Estimate	*Std. error*	*z value*	*Pr(>|z|)*
Artificial developmental site model				
(Intercept)	−0.43	0.25	−1.69	0.09.
Organic content (linear)	1.83	0.37	4.89	$1.01e^{-06}$***
Organic content (quadratic)	−0.49	0.31	−1.58	0.11
Clearness (linear)	−1.54	0.52	−2.94	0.003**
Clearness (quadratic)	0.45	0.39	1.16	0.24
Shade	1.20	0.21	5.78	$7.41e^{-09}$***
Depth (linear)	1.34	0.33	4.04	$5.30e^{-05}$***
Depth (quadratic)	−0.20	0.31	−0.63	0.53
Natural developmental site model				
(Intercept)	1.13	0.32	3.49	0.00***
Organic content (linear)	0.97	0.54	1.78	0.007**
Organic content (quadratic)	−0.78	0.52	−1.49	0.14
Clearness (linear)	−0.66	0.48	−1.37	0.17
Shade	0.41	0.32	1.29	0.20
Depth (linear)	1.05	0.47	2.23	0.03*
Depth (quadratic)	−0.97	0.46	−2.11	0.03*

Statistical significance: .0.1; *0.05; **0.01; ***0.001.

however, the quadratic effect was lower than the linear one ($p = 0.019$, $p = 7.10e^{-06}$, respectively). The GCD of the model was 0.19.

DISCUSSION

This study represents the first report on *Ae. albopictus* larval habitats and geographic distribution during a severe CHIKV epidemic. The findings confirm that *Ae. albopictus* was the sole vector independent of season on the island of La Réunion.

During the winter of 2005, *Ae. albopictus* was found at altitudes up to 800 m throughout most of La Réunion, except in the southeast, where roads were at lower elevations and no sampling was carried out, and in Tampon (1200 m), the only site where *Ae. albopitus* was observed at a higher elevation. Only the central high plateau of the island and high-elevation populated areas (gray areas on the map in Fig. 1) located on the west part of the island were free of mosquitoes in winter. The lowest average temperature (12.6°C) where *Ae. albopictus* was observed (1080 m) was in the western part of the island, showing the good capacity of this vector for adaptation to different ecological zones and a strong tolerance to low temperatures. The geographical distribution was determined by scoring the presence of *Ae. Albopictus*; however, no population densities were recorded. The density factor is an important criterion of differentiation between the winter and summer seasons and would therefore be important to study in evaluating the vector risk and better planning vector-control campaigns during different seasons.

As described in the literature (Hawley 1988), the microhabitat of *Ae. albopictus* consists of a wide range of container types, from natural to artificial. Similar results were found in this study. Larvae were found in containers with volumes varying from 1 ml to 200 l. Over all, the containers (with water) with observed pupae presence were predominantly used tires and barrels (Focks 2003; Focks and Alexander 2006; Mori 1979). For the most part, the same factors were significant for pupae presence with the GLM model, so that clear water with organic content (medium to high), medium depth, and in a shaded container provided the most suitable place for *Ae. albopictus* pupae presence.

During the winter survey in peri-urban areas and gullies, *Ae. albopictus* was predominantly found in natural developmental sites. Gomes Ade et al. (1995), in a similar study for the development of larvae of *Ae. Albopictus*, had shown that the mortality of larval and pupal stages was lower in natural containers than in artificial ones. Food availability, usually greater in natural containers than in artificial ones, has been shown to be of primary importance to larva survival and adult sizes (Hawley 1988).

The results of the GLM models also showed that clear water with organic content (medium to high), at a medium depth and in a shaded container provided the best suitable larval and pupal development site for *Ae. Albopictus*. These results are in agreement with other studies. Indeed, Sunhara and Mogi (2002) showed that high organic content, such as leaf-litter input, moderates the inhibitory priority effects on *A. albopictus* larvae, not only by supplying food resources but also by alleviating the toxicity of accumulated dissolved substances. Also, other organic content, such as invertebrate carcasses, have also been found to favor larvae development (Daugherty et al. 2000).

In this study, containers were observed for the presence or absence of larvae or pupae and the actual productivity of sites (Focks et al. 1995, Tun-Lin et al. 1996) were not accessed. That being said, the *Ae. albopictus* immatures, in both urban and peri-urban sites were observed most often in waste containers, flower plates, and used tires. Tree holes filled with water were rarely observed in our surveys, probably because we carried them out during the dry cold season. The natural sites most frequently infested in the peri-urban and gully areas were bamboo stumps and rock holes. Bamboo stumps had already been described as one of the three common habitat types for *Ae. albopictus* in Asia and some Oceanic islands (Hawley 1988), and it can be extended to the islands of the Indian Ocean. Dry climatic conditions prevent growth of bamboo trees in the gully in west part of the island. Therefore, all positive bamboo stumps were observed on the east side of the island. Bamboo stumps were often found positive for larvae or pupae; unfortunately they are not very accessible for vector control. However, very high quantities of artificial developmental sites in the urban areas were found during the survey (513 positive containers for 750 houses visited). Most of the domestic and peri-domestic containers are associated with water storage and produce mosquitoes year round. This situation creates very favorable conditions for arbovirus circulation, not only the CHIKV, but also other arboviruses already present in or introduced to the region. Indeed, a serious Dengue epidemic occurred in La Réunion in 1977 that affected up to 35% of the island's inhabitants (Coulanges et al. 1979, Kles et al. 1994). That epidemic was assumed to be vectored by *Ae. albopictus*. Since then, no epidemic dengue transmission has been reported in La Réunion, despite the low-level circulation of Dengue 1 virus since 2004. *Aedes albopictus* shows great ecological plasticity, with a distribution across different ecosystems, altitudes, and seasonal extremes (as low as 12.6°C in our study) and therefore is a real threat to La Réunion and all the other islands in the area. Population biology studies of this major pest are of primary importance to evaluate risks for new parvovirus outbreaks and for developing adequate vector-control measures.

ACKNOWLEDGMENTS

The authors thank Frédérique Chiroleu for advice on the model construction and critical reading of the model part of the manuscript. They also thank Samuel Huet and Abdulh Rutée for invaluable help with the fieldwork and Paul Reiter for critical reading of the manuscript. This work was funded in part by the Institut de Recherche pour le Développement (IRD), Centre de Cooperation Internationale en Recherche Agronomique pour le Développement (Cirad), and Direction Régionale des Affaires Sanitaires et Sociales (DRASS). Finally, the authors thank two anonymous reviewers and the journal editor for recommending improvements to the manuscript.

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