

Aedes (Diptera: Culicidae) Vectors of Arboviruses in Mayotte (Indian Ocean): Distribution Area and Larval Habitats

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ABSTRACT Biological invasions generally induce profound effects on the structure of resident communities. In Mayotte, where *Aedes aegypti* and *Ae. lilii* were already present, the recent introduction of *Ae. albopictus* raises public health concerns because it may affect the risk of arbovirus transmission. Entomological surveys were carried out in six locations on the island following a transect defined by a gradient from urban to rural habitats during a dry and a wet season. A total of 438 larval habitats containing *Aedes* spp. immature stages were surveyed. We evaluated the characteristics of larval habitats and analyzed the field distribution of *Aedes* spp. throughout Mayotte using generalized linear models. Artificial containers used for water storage were significantly more productive for *Ae. albopictus* immature stages than for *Ae. aegypti* ones. Most of natural larval habitats collected were colonized by *Ae. aegypti*, and it was also the most common *Aedes* species encountered in rural habitats. Conversely, *Ae. albopictus* greatly predominated in urban and suburban habitats and during the dry season. *Ae. lilii* was uncommon and occurred preferentially in leaf axillae and dead leaves on the ground. *Ae. albopictus* has rapidly colonized the inhabited areas of Mayotte. A displacement of *Ae. aegypti* populations by *Ae. albopictus* populations in urban areas might be happening. The increasing urbanization seems to greatly favor the presence of the invasive species. Thus, arbovirus surveillance programs should focus, as a priority, on areas where this vector is present because of a higher risk of emergence of an epidemic source of arboviruses.

KEY WORDS *Aedes albopictus*, *Aedes aegypti*, *Aedes lilii*, larval ecology, Mayotte

Aedes (*Stegomyia*) *aegypti* L. (Diptera: Culicidae) is native to Africa where the ancestral form, *Ae. aegypti formosus*, is sylvatic and implicated in enzootic pathogens transmission (McClelland 1968, Tabachnik and Powell 1979). The domesticated form, *Ae. aegypti aegypti*, breeding specifically in domestic environments, had spread to the Americas with the slave trade, whereas in Asia, its distribution followed trade and colonization routes (Tabachnik and Powell 1979, Halstead 2007). Now the species is considered widespread in tropical and intertropical countries between latitudes of 45° N and 35° S. *Ae. aegypti* is arguably recognized as the major vector of yellow fever and dengue viruses (Christophers 1960), which are of major importance in terms of human health: ≈2 billion humans are at risk of infection with one or more of the four dengue viruses.

Aedes (*Stegomyia*) *albopictus* (Skuse), the “Asian tiger mosquito,” is native to Southeast Asia. For the last 30 yr, this species has progressively adapted to human environments and has spread from its native area. It was first found in Albania in 1979 (Adhami and Murati 1987), and then it was recorded in the United States (Sprenger and Wuithiranyagool 1986), Brazil, and Mexico during the 1980s (Benedict et al. 2007). It was also found in Cuba, Honduras, Bolivia, Argentina, Colombia, and Paraguay between 1995 and 1998; the species is now widespread in the North and South American continents (Benedict et al. 2007). *Ae. albopictus* has also been reported in Belgium, France (Schaffner et al. 2001), Italy (Dalla Pozza and Majori 1992), and Switzerland in Europe, from Israel in the Middle East, and from Cameroon, Equatorial Guinea, and Nigeria in Africa (Hawley 1988, Gratz 2004, Benedict et al. 2007). Its colonization of new areas was facilitated by the increase in human displacements and intercontinental trades. Worldwide, the trade in used tires has been implicated as the primary dispersal mechanism of this species (Reiter 1998). Indeed, used tires constitute important laying sites in which eggs can subsist for several weeks. *Ae. albopictus* is a competent vector for at least 22 arboviruses, notably dengue (all four serotypes), Chikungunya (Vazeille et al.

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2007), Ross River, LaCrosse, and others (Shroyer 1986).

Aedes aegypti and *Ae. albopictus* are both container-breeding mosquitoes found in a wide range of containers types. They are known to be very common in inhabited areas. In Southeast Asia, *Ae. aegypti* preferentially occupies artificial containers situated indoors (Christophers 1960), whereas *Ae. albopictus* breeds preferentially in natural container-like tree holes, bamboos stumps, and sometimes artificial containers like tin cans and tires (Hawley 1988). Nevertheless, in many countries with co-occurrence of these species such as Brazil, the United States, Singapore, and Cameroun (Chan et al. 1971a, Braks et al. 2003, Simard et al. 2005), *Ae. aegypti* and *Ae. albopictus* often share the same larval habitats. A recent study on *Ae. albopictus* microhabitats characteristics in La Réunion island showed that this species colonizes several types of water containers from artificial to natural ones and shows a preference for shady containers filled with clear water with little organic content (Delatte et al. 2008a). In its native area, the most critical factor for the occurrence of *Ae. albopictus* is the presence of vegetation (Chan et al. 1971b, Nguyen et al. 1974), which explains that this species mainly occurs in suburban and rural areas (Tewari et al. 2004). Conversely, *Ae. aegypti* is commonly encountered in urban areas in many parts of the world (Christophers 1960, Hornby et al. 1994, O'Meara et al. 1995).

The installation of *Ae. albopictus* in some islands of the southwestern Indian Ocean (ISIO) dates back to several centuries, in connection with human population migratory episodes from Southeast Asia. In La Réunion, this species was recorded for the first time in 1913 (Edwards 1920) and is now the most common *Aedes* species encountered on this island (Hamon 1953). Conversely, *Ae. aegypti* is rare in La Réunion and only persists as residual populations restricted to a few locations (Salvan and Mouchet 1994). *Ae. albopictus* is also present in Mauritius where *Ae. aegypti* is virtually absent, on the Eastern coast of Madagascar (Fontenille and Rodhain 1989), in Rodrigues, and in the Seychelles (Metselaar et al. 1980, Julvez et al. 1998). A recent study apparently mentioned changes in *Ae. albopictus* distribution in Madagascar, where it is now also found on the west coast (Delatte et al. 2008b).

In Mayotte, Brunhes (1978) recorded 35 species of Culicidae in 1978 belonging to eight genera: *Anopheles*, *Culex*, *Eretmapodites*, *Mansonia*, *Orthopodomyia*, *Ficalbia*, *Uranotaenia*, and *Aedes*. In the latter genus, he mentioned three *Stegomyia* species: *Ae. vittatus* (Bigot), *Ae. aegypti*, and *Ae. simpsoni* (Theobald). In Central Africa and Cameroon, *Ae. vittatus* preferentially develops in natural larval habitats like tree holes and is suspected to have been linked with yellow fever epidemics in Nigeria and Soudan in 1969 (Brunhes 1978). *Ae. aegypti* was recorded for the first time in Mayotte in 1943 and is suspected to have been the major vector of a supposed Dengue epidemic fever that raged throughout the island during this year (McCarthy and Brent 1943). No data in the literature

mentioned the *Ae. aegypti* form that occurred in Mayotte. *Ae. (Stegomyia) simpsoni* (Theobald) was incriminated as one of the primary vectors of yellow fever virus among primates, including humans, during the 1940s. It was probably the primary vector of yellow fever virus in Africa. Huang (1979) described *Ae. simpsoni* as a complex of at least three species: *Ae. simpsoni*, *Ae. bromeliae*, and *Ae. lili*. *Ae. bromeliae* is common throughout most of the Afrotropical region. It is also mentioned in the Comoros archipelago (more precisely in Grande Comore). No study mentions which species of the Simpsoni complex occurs in Mayotte. Larvae of this species were encountered equally in both urban and rural areas (Brunhes 1978). The presence of *Ae. albopictus* in Mayotte was first recorded in 2001 (Girod 2004), but no information was given concerning its distribution on the island.

In 2005–2006, a Chikungunya epidemic raged in Mayotte, affecting 38% of the population (Cire Mayotte 2007). The presence of *Ae. albopictus* in the island probably played an important role in emergence of this infectious disease. In addition to ecological problems linked to the introduction of *Ae. albopictus*, some serious public health risks could have appeared because this species is an aggressive pest and an efficient disease vector (Benedict et al. 2007). Mitchell (1995) suggested that the introduction of *Ae. albopictus* in a new area could affect the resident mosquito populations and the transmission of arboviruses. The emergence of Chikungunya in Mayotte has underlined our drastic lack of knowledge on the vector's ecology. The vector implicated in the transmission of the disease has not been precisely identified, although it was most probably *Ae. aegypti* or *Ae. albopictus* because they are the major vectors known for the transmission of this virus. This study aims to determine the ecological niche that is being colonized by *Ae. albopictus* in Mayotte to better understand its adaptation to this new environment and its potential role in the transmission of Chikungunya. Our purpose was also to update the data on the distribution of *Ae. aegypti* and other *Aedes* spp. in Mayotte and to improve our knowledge of their larval ecology.

Materials and Methods

Study Area and Collection Sites. Mayotte (12°45'43 S; 45°12'25 E) is a French island (376 km²) in the Indian Ocean, belonging to the Comoros archipelago, situated in the Mozambique Channel. It is composed of two islands 1 km apart: Grande Terre, the main island, which culminates at 660 m, and Petite Terre, an islet where the airport is installed (Fig. 1). Mayotte has a maritime tropical climate with two distinct seasons: a cool and dry winter from May to October and a warmer, rainy summer from November to April.

Surveys were conducted in six localities of Mayotte chosen on Grande Terre (Mtsapere, Bandrele, Mtsamoudou, Chiconi, Dzoumogne) and Petite Terre (Labattoir).

Two entomological surveys were conducted in 2007: one during the rainy austral summer (5 to 20

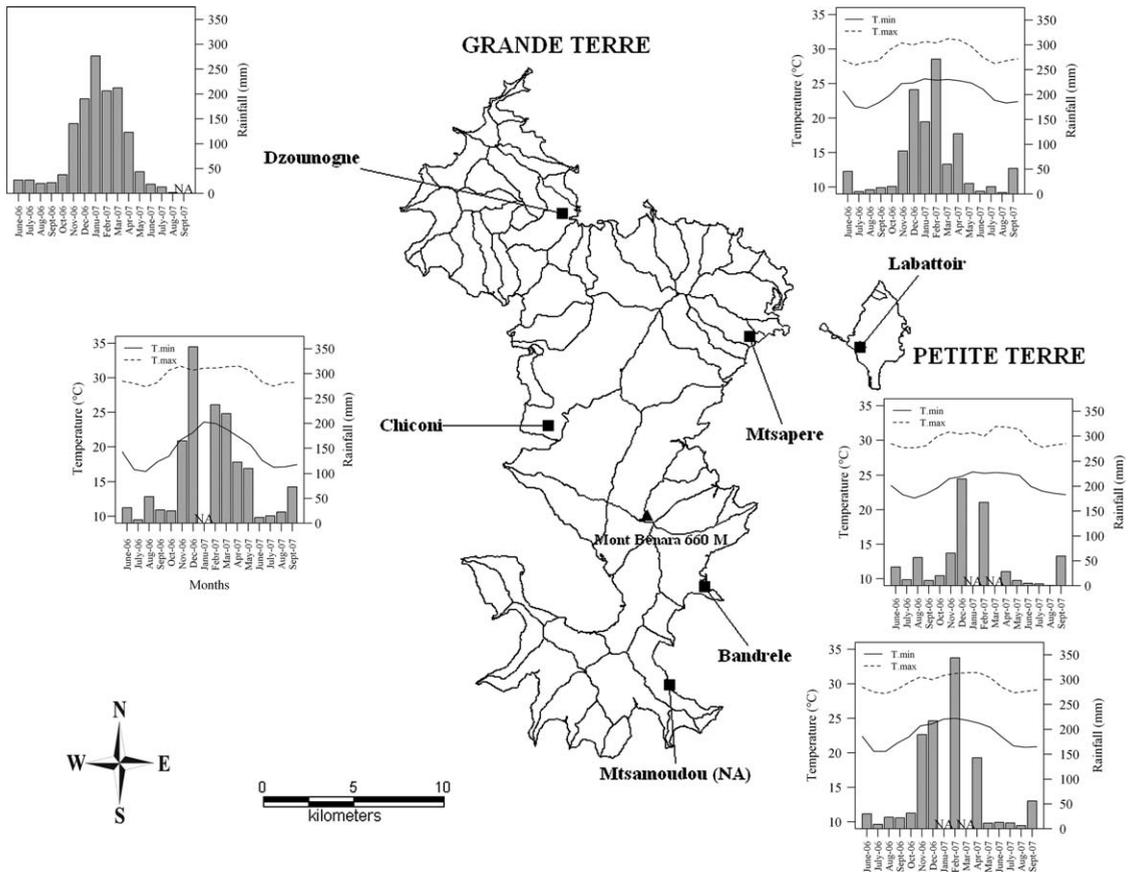


Fig. 1. Average rainfall and minimum and maximum average temperature data for the six localities sampled in Mayotte.

March 2007) and the other one during the dry winter (between 21 August and 9 September 2007). The average monthly rainfall and the average monthly minimal and maximal temperatures from June 2006 to September 2007 of five of the six locations sampled were obtained from Météo France Mayotte (Fig. 1). There is little local variation in monthly temperatures from east coast to west coast. Nevertheless, the east coast is the driest one and the west coast is the wettest (Raunet 1992). The annual rainfall in the center, the north, and the northwestern coast varies from 1,300 to 1,800 mm, whereas the south and southeastern coast receive ~800–1,200 mm rainfall per year.

In each site, sampling was performed following a transect defined by a gradient from urban, through suburban, to rural habitat. The parameters used for the characterization of habitats was the number of houses and the vegetation density. The number of houses increased from rural to urban habitat, whereas vegetation density decreased. In fact, in urban areas, the houses were close to each other with few or no vegetation in yards; in suburban areas, the houses were less numerous with more vegetation in bigger yards. Rural habitats, characterized by the absence of houses, were generally cultivated with bananas or

coconut trees. In this type of habitat, 1 ha chosen around a central point, which was georeferenced with a GPS unit (Garmin, eTrex, Romsey, United Kingdom), was thoroughly sampled. In urban and suburban areas, 10 positive georeferenced houses were sampled. A house was recorded as positive when at least one larval habitat present in the yard contained an immature stage of any *Stegomyia* spp. (*Ae. aegypti*, *Ae. albopictus*, or *Ae. simpsoni*). For each sample collected, three environmental parameters (location, type of habitat, and season) were recorded.

Sampling of Immature Stages. Only containers with *Aedes* spp. immature stages were recorded during this survey. For all of them, the depth, the width, and the volume were measured (Table 1). These microhabitats were also defined by visual characteristics like the organic content, the water quality, and the sunshine exposure.

All larvae and pupae from each mosquito-positive container were collected, counted, and brought back to the regional vector control laboratory (DASS Mayotte). Larvae were preserved in alcohol and identified with published taxonomic keys (Hopkins 1952, Brunhes 1978, Huang 1979), whereas pupae were main-

Table 1. Mean depth and width of each type of larval habitat

Larval habitats	N	Mean width (±SE) (cm)	Depth width (±SE) (cm)
Natural			
Leaf axilla	19	2.5 ± 0.22	1.1 ± 0.11
Snail shells	2	3.0 ± 1.00	2.0 ± 1.00
Coconut shells	44	6.7 ± 0.64	2.4 ± 0.31
Tree holes	16	6.8 ± 0.85	12.1 ± 8.03
Dead leaves on ground	26	7.2 ± 0.60	1.3 ± 0.15
Rock holes	6	10.2 ± 2.01	3.5 ± 0.81
Bamboo stumps	10	10.7 ± 0.94	19.2 ± 3.80
Artificial			
Small plastic wastes	27	5.7 ± 0.95	3.0 ± 0.69
Tin cans	21	7.1 ± 0.75	2.6 ± 0.44
Broken bottles	20	8.4 ± 0.53	5.8 ± 0.78
Others	25	13.6 ± 1.76	4.4 ± 1.22
Used tires	10	10.3 ± 0.42	4.2 ± 0.57
Earthenware jars	5	14.4 ± 1.44	4.6 ± 2.16
Cans	24	14.8 ± 1.17	6.3 ± 1.58
Pots	68	20.3 ± 1.02	3.3 ± 0.41
Buckets	46	25.9 ± 0.89	9.8 ± 2.05
Barrels	69	51.6 ± 0.66	15.4 ± 1.87

tained in the laboratory until adult emergence allowed identification. Adults of *Ae. aegypti* collected during our survey were identified morphologically as *formo-*

sus form according to McClelland's morphological criteria (McClelland 1968). Adults of the *Ae. simpsoni* complex collected during our survey were identified as *Ae. lilii* using Huang's determination key (Huang 1979).

For each type of container, the larval productivity defined as the average number of larvae per container and the pupal productivity defined as the average number of pupae per container were calculated (Fig. 2). The efficiency of a container type was also calculated and defined as the proportion of pupae produced by the container type divided by the prevalence of that container type (Table 2).

Statistical Analysis. The productivity of artificial larval habitats (also coconut shells) for larvae of both species was compared using nonparametric tests (Kruskal-Wallis rank sum test and Wilcoxon test). In fact, there were not enough natural larval habitats and larval habitats containing pupae to allow us to compare their productivity using statistical analysis. The data on *Aedes* spp. (presence or absence of *Ae. aegypti*, *Ae. albopictus*, or *Ae. lilii*) were analyzed using a generalized linear regression model (GLM) with binomial distribution and logit link as a function of all

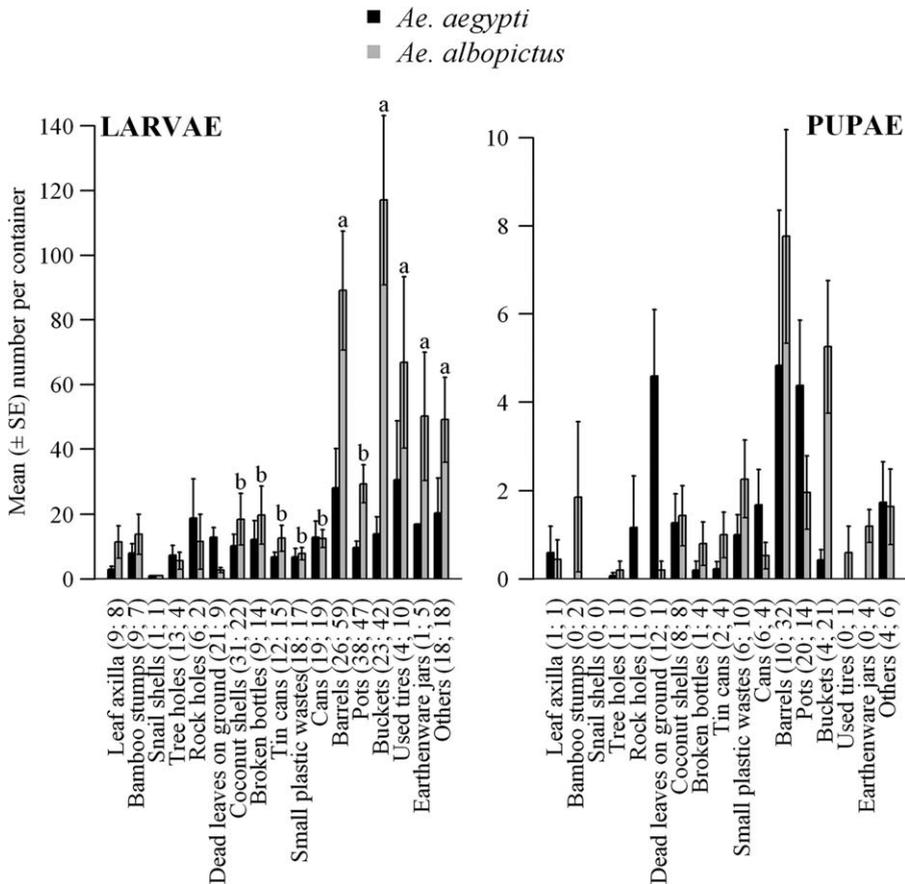


Fig. 2. Average productivity of larval habitats for *Ae. aegypti* and *Ae. albopictus* larvae and pupae. (a and b) Significant difference of average productivity for *Ae. albopictus* larvae (Wilcoxon test, $P < 0.05$). On the abscissa, larval habitat name followed by (n containing *Ae. aegypti*, n containing *Ae. albopictus*).

Table 2. Efficiency of larval habitats for *Ae. aegypti* and *Ae. albopictus*

Larval habitats	<i>Ae. aegypti</i>				<i>Ae. albopictus</i>			
	Containers (n)	Pupae (n)	Max. ^a	Efficiency ^b	Containers (n)	Pupae (n)	Max. ^a	Efficiency ^b
Leaf axilla	1	6	6	0.8	1	4	4	0.5
Snail shells	0	0	0	0.0	0	0	0	0.0
Coconut shells	8	42	20	0.7	8	33	14	0.5
Tree holes	1	1	1	0.1	1	1	1	0.1
Dead leaves on ground	12	101	22	1.1	1	2	2	0.2
Rock holes	1	7	7	0.9	1	0	0	0.0
Bamboo stumps	0	0	0	0.0	2	13	12	0.8
Small plastic wastes	6	18	6	0.4	10	43	15	0.5
Tin cans	2	3	2	0.2	4	15	6	0.4
Broken bottles	1	2	2	0.2	4	12	7	0.3
Others	4	33	15	1.0	6	36	16	0.7
Used tires	0	0	0	0.0	1	6	6	0.7
Earthenware jars	0	0	0	0.0	4	6	2	0.2
Cans	6	32	12	0.7	4	10	5	0.3
Pots	20	197	40	1.2	14	92	36	0.8
Buckets	4	10	4	0.3	21	226	47	1.2
Barrels	10	145	106	1.8	32	489	95	1.8
Total	76	597	243		114	988	268	

^a Maximum *n* pupae in an individual container.

^b Efficiency = productivity (*n* pupae per container × 100/total pupae)/prevalence of container (*n* containers × 100/total containers).

environmental factors (location, type of habitat, and season), all characteristics of larval habitats and interactions. The characteristics studied were type of developmental site (artificial or natural), clearness of water (clear, tinted, turbid), organic content rate (small, medium, high), shade (yes, no), depth (small: <3 cm; medium: 3–9.9 cm; high: >10 cm), width (very small: <5 cm; small: 5–10 cm; medium: 10–20 cm; high: 20–40 cm; very high: >40 cm), and volume (very small: <100 ml; small: 100–500 ml; medium: 500–1,000 ml; high: 1,000–10,000 ml; very high: >10,000 ml). Four generalized logistic models were built to explain the following binary variables: larval habitats with only *Ae. aegypti*, larval habitats with only *Ae. albopictus*, larval habitats with both species, and larval habitats with *Ae. lili*.

We used the backward/forward stepwise procedures, which used Akaike's Information Criterion (AIC), to obtain the best model (Burnham and Anderson 1998). The AIC value changed between models tested, and the model with the lowest AIC value represented the best model fit (Burnham and Anderson 1998). We started from the most complex model (including environmental factors and characteristics of larval habitats). The best model resulting enabled us to predict the relative frequencies of *Ae. albopictus* and *Ae. aegypti* corresponding to the proportion of microhabitats with *Ae. albopictus* or *Ae. aegypti* of all larval habitats collected containing *Aedes* spp. immature stages.

The effects of nonsignificant factors were analyzed by one-way analysis of variance (ANOVA) made on a linear model built from the residuals of the GLM. The best model was given directly by the function step.

Results

In total, 438 water collections containing immature stages of *Ae. albopictus*, *Ae. aegypti*, or *Ae. lili* were

examined from the six locations sampled, among which 428 (97.7%) were colonized by immature stages of *Ae. aegypti* or *Ae. albopictus*. Only a few larval habitats were found to contain *Ae. lili* (59/438; i.e., 13% of samples). Less than 10 larval habitats containing *Ae. vittatus* were found in rural areas in tree holes during the rainy season. The presence of this species in our sampling was so rare that we will not mention it in this paper. *Ae. albopictus* was more common than *Ae. aegypti* and occurred in 315 larval habitats compared with 276 for *Ae. aegypti*. Both species were found together in 37% of the larval habitats sampled (163/438). The presence of both species was conditioned by environmental factors (season, location, and habitats). In fact, the best model resulting from the most complex model included only environmental variables as significant factors for the presence of species.

Characteristics of Larval Habitats of *Aedes* spp. Larval habitats sampled were classified and characterized depending on their nature, width, and depth (Table 1). There were 316 artificial containers and 122 natural containers. More than 75% of the natural larval habitats collected, particularly coconut shells and dead leaves on the ground, were occupied by *Ae. aegypti*. *Ae. albopictus* was significantly more frequent in artificial containers and was rarely found in natural larval habitats except coconut shells (proportion test, $P < 0.0005$). *Ae. lili* was most common in natural larval habitats (54%) such as leaf axillae and dead leaves on the ground.

Indeed, each type of larval habitats did not show the same productivity for both species (Fig. 2). Artificial sites produced significantly more *Ae. albopictus* larvae than *Ae. aegypti* larvae (Wilcoxon test, $P < 0.05$). Larval habitats containing *Ae. aegypti* larvae produced between 3 and 31 larvae on average; the mean productivity of these breeding sites (i.e., the average number of larvae per container) did not significantly

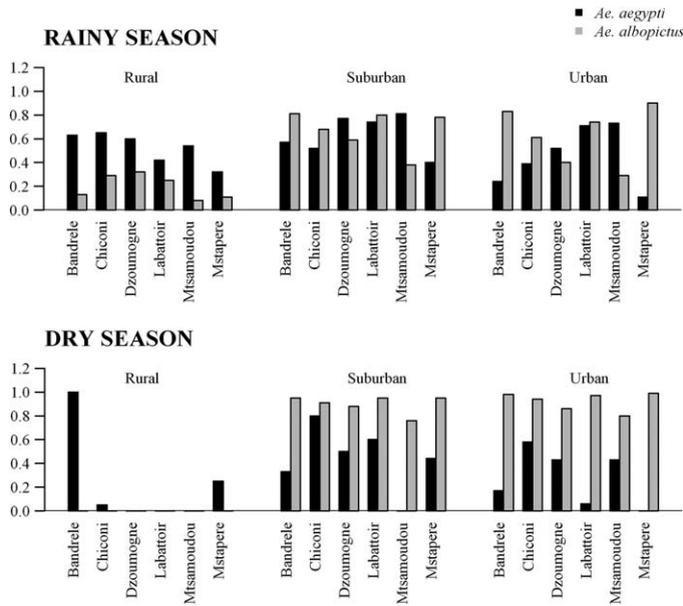


Fig. 3. Estimated relative frequency of larval habitats containing *Ae. aegypti* and *Ae. albopictus* during the rainy and dry seasons in each location for each habitat.

differ from each other (Kruskal-Wallis rank sum test, $P > 0.05$; Fig. 2). For *Ae. albopictus*, two groups of larval habitats with a significant difference in productivity could be observed (Kruskal-Wallis rank sum test, $P < 0.05$; Wilcoxon test, $P < 0.05$). The first group, with a mean depth < 5.5 cm, was composed of coconut shells, broken bottles, tin cans, small plastic wastes, cans, and pots that produced between 5 and 33 larvae on average. The second group, with a mean width > 13 cm, was composed of wider artificial containers such as barrels, buckets, used tires, earthenware jars, and voluminous wastes, which produced on average > 40 larvae (Fig. 2; Table 1).

Dead leaves on the ground, barrels, and pots produced the highest quantity of *Ae. aegypti* pupae, and they also showed the highest container efficiencies (> 1). For *Ae. albopictus*, barrels and buckets were the most productive for pupae, and they were the most efficient containers. Nevertheless, because only a few of the larval habitats sampled contained pupae, no significant differences between containers productivity for *Ae. albopictus* and *Ae. aegypti* pupae were found (Fig. 2).

To understand precisely the effects of characteristics of larval habitats, we built a linear model from residuals of our best model. This linear model showed that occurrence of *Ae. albopictus* in a larval habitat depends on the depth and organic content observed for the container. This species was more often found in larval habitats with a depth > 10 cm and a low organic content rate. Larval habitat characteristics were not discriminating enough to explain the presence of *Ae. aegypti*. The co-occurrence of both species in a larval habitat depended on width and organic content rates observed. They were commonly found

together in wide containers (20–40 cm) with a high organic content rate. *Ae. lili* occurrence in a larval habitat depended on the nature of this site and the presence of *Ae. aegypti* in it. Seventy-six percent of larval habitats containing this species also contained *Ae. aegypti* immature stages.

Distribution of *Aedes* spp. We used GLM to fit presence/absence of species as a function of season, location, habitat, and interactions. Our model enabled us to predict the relative frequencies of *Ae. albopictus* and *Ae. aegypti* for all seasons, locations, and habitats. They are presented in Fig. 3, and they correspond to the frequency (relative to *Aedes* spp.) of *Ae. aegypti* and *Ae. albopictus* in locations and habitats during each season.

During the rainy season, *Aedes* spp. were found in all locations and habitats sampled (Fig. 3). There were significantly more larval habitats collected with *Ae. aegypti* immature stages than larval habitats with *Ae. albopictus* (228 and 200, respectively; proportion test, $P < 0.02$). During the dry season, there were significantly fewer larval habitats found (123 instead of 315 during the rainy season).

The relative frequency of *Ae. aegypti* was best fitted by the model that included all environmental factors season, habitat, and location and interactions between habitat, location, and season. Therefore, the frequency of occurrence of *Ae. aegypti* depended on the habitat, the location, and the season considered at the same time. This species was present in all locations and habitats during the rainy season, but it was the most common *Aedes* encountered in rural areas. It was found in $> 80\%$ of larval habitats sampled in this habitat. Relative frequency of *Ae. aegypti* decreased during the dry season, but it was still the most common

species in rural areas even if just few larval habitats were collected there. Indeed, *Ae. aegypti* was also found in urban habitats (relative frequency > 50%) at three of the six locations during the rainy season: Dzoumogne, Labattoir, and Mtsamoudou.

For *Ae. albopictus*, the factors season, habitat, location, and interactions season and habitat and location and habitat were all significant, which implies that the relative frequency of *Ae. albopictus* also depends on habitat, season, and location at the same time. *Ae. albopictus* was relatively rare in rural habitats but largely present in other habitats across all locations (it occurred in 115 larval habitats of 122 sampled); it was the most frequent *Aedes* species encountered in urban and suburban habitats. It occurred in >80% of larval habitats sampled in these types of habitat during the rainy season in Bandrélé, Labattoir, and Mtsapéré. During the dry season, the relative frequency of *Ae. albopictus* in urban and suburban habitats significantly increased in all locations (proportion test, $P < 0.05$), and it was found in >80% of *Aedes* larval habitats collected there.

The significant factors for co-occurrence of both species were season, habitat, location, and the interactions season and habitat and season and location. Larval habitats with both species predominated in suburban areas during the rainy and dry seasons. During the rainy season, >40% of *Aedes* spp. larval habitats collected in suburban areas contained immature stages of both species simultaneously.

The relative frequency of *Ae. lili* was best fitted by the model that included all environmental factors season, habitat, and location. Eighty-eight percent of larval habitats containing *Ae. lili* were found during the rainy season. It occurred mainly in rural (47%) and suburban habitats (42%).

Discussion

This study updates *Stegomyia* distribution in Mayotte and preferential habitats of the invasive species *Ae. albopictus*, 6 yr after its first record on the island. This species has now spread throughout Mayotte, and it has been found in all locations and habitats of the island. Nevertheless, it is difficult to assess the date of introduction of *Ae. albopictus* in Mayotte because no entomological detailed data had been recorded between 1977 and 2000. It probably occurred during the invasion phase of this species all over the world, i.e., during 1980–2000 (Hawley 1988, Lounibos 2002).

During our survey, *Ae. albopictus* predominated in urbanized habitats, whereas *Ae. aegypti* and *Ae. lili* were most common in rural ones. In Southeast Asia, where *Ae. aegypti* and *Ae. albopictus* also live in sympatry, they rarely share exactly the same habitat (Hawley 1988). In fact, *Ae. albopictus* is mainly found in rural areas (Tsuda et al. 2006) and in outdoor larval sites (Hawley 1988, Thavara et al. 2001), whereas *Ae. aegypti* that has invaded occurs principally in urban habitats (Harrington et al. 2001). In these regions, the increase in abundance of *Ae. aegypti* was accompanied by a decrease in the abundance of the native *Ae.*

albopictus (Rudnick and Hammon 1960, Gilotra et al. 1967, Chan et al. 1971a, Hawley 1988). The displacement of *Ae. albopictus* by *Ae. aegypti* in Southeast Asia may have been caused by the destruction of *Ae. albopictus* rural habitats with a concomitant increase in urban habitat more suitable for *Ae. aegypti* with more indoor sites (Chan et al. 1971b, Hawley 1988). In Brazil and Florida (O'Meara et al. 1995, Braks et al. 2003, Lima-Camara et al. 2006), in Puerto Rico (Cox et al. 2007), and in most countries where *Ae. albopictus* was the invader, the same scenario happened: *Ae. albopictus* was very common in more rural habitats and *Ae. aegypti* seemed to be more adapted to urban ones. To explain displacement occurring in these different countries, some authors hypothesized a competitive interaction between *Ae. albopictus* and *Ae. aegypti*, the outcome of which depends on areas and species strains considered (Rudnick and Hammon 1960, Gilotra et al. 1967, Braks et al. 2003).

In Mayotte, the distribution of both species is different from elsewhere, probably because of the occurrence of *Ae. aegypti formosus* instead of *Ae. aegypti aegypti*, even if the species seems to be adapted to urban areas in this island. To understand the situation in Mayotte, two hypotheses can be made. First, we can hypothesize that the arrival of *Ae. albopictus* in the island could have occurred in parallel with its urbanization, inducing this species to settle down in an available niche that was probably under colonization by *Ae. aegypti* (Subra and Hebrard 1977). Moreover, in this island, even in urban areas, most of the larval habitats are situated outdoors, which is described to be *Ae. albopictus* favorite sites to develop (Hawley 1988, Thavara et al. 2001). The second hypothesis supposes a competitive displacement from urban to rural habitat of *Ae. aegypti* population that had colonized urban areas before *Ae. albopictus*. To test these hypotheses, further studies would be necessary. Nevertheless, it will be difficult to describe precisely what occurred in Mayotte considering the lack of data on the distribution and abundance of *Ae. aegypti* there before the arrival of *Ae. albopictus*.

We identified *Ae. lili* in Mayotte using Huang's determination key (Huang 1979). This species occurs across Africa but is less common than the two others species of the complex. It has been described in southeastern Sudan, in western Ethiopia, and in the south of Uganda. Larvae of *Ae. lili* have been collected from axils of *sanseveria* (Liliaceae) in Uganda. Females of this species are not known to bite humans (Huang 1979), and, during our field samplings, we have never been bitten by females of this species. In our study, *Ae. lili* was mainly found in natural larval habitats as is the case for other species of the complex in central Africa and Cameroon (Pajot 1976, 1978). The occurrence of this rural species in Mayotte is rare, and its lack of interest for human blood does not rank it as an important arbovirus vector on the island.

Restrictive abiotic factors (such as temperature and humidity) could also explain the spatial or temporal segregation between *Ae. aegypti* and *Ae. albopictus*. In fact, in Madagascar, Fontenille and Rodhain (1989)

made this hypothesis because *Ae. albopictus* was found on the wetter coast and *Ae. aegypti* on the drier one. Juliano et al. (2002) proposed that warm dry climates favor *Ae. aegypti* by alleviating the effects of competition from *Ae. albopictus* through differential mortality of *Ae. albopictus* eggs. However, in our survey, *Ae. albopictus* prevailed throughout the year, even during the dry season at a relatively constant level, perhaps because its major larval habitats were human-made water storage containers used for ablution, which were regularly filled with water. These containers (barrels and buckets) were the most common larval habitats encountered in premises yards in a close space used for ablution and in urban and suburban areas. However, *Ae. aegypti* populations, breeding primarily in natural sites outdoors, were markedly affected in the dry season when these sites are mostly dry. This species might survive at the egg stage during this season because this stage is more resistant to desiccation (Juliano et al. 2002).

In Mayotte, *Ae. albopictus* was more frequently found to develop in artificial larval habitats. This result contrasts with previous studies from Southeast Asia where this species is mentioned in a wide range of container types from natural to artificial (Hawley 1988), with a preference for natural larval habitats like bamboo stumps and tree holes. Many studies also described used tires as one of the main larval habitats and presumably one of the most productive for *Ae. albopictus* (Adhami and Reiter 1998, Reiter 1998). In many countries, used tires and barrels were also predominant containers with observed pupal presence (Mori 1979, Focks et al. 1995, Focks and Alexander 2006, Delatte et al. 2008a), which is similar to our findings except for used tires. In our survey, few used tires were sampled because they were not frequent in yards. Among natural larval habitats sampled, coconut shells were the most common natural larval habitats encountered in rural but also in urban and suburban areas as coconut constitutes a staple food for local population. Coconut husks are usually kept outdoors near houses for long periods of time and are usually infested by *Aedes* spp. or *Eretmapodites* spp., especially during the rainy season. They were also considered to be one of the highly productive larval habitats for *Ae. albopictus* in Samui Island in Thailand (Thavara et al. 2001).

In general, an exotic species succeeds in colonizing new regions because of both its capacity to adapt to new environmental conditions and to compete with preexisting species. Most available studies suggest that the invasion by *Ae. albopictus* triggers a decline in the abundance of *Ae. aegypti* and may even lead to its disappearance because both species often share the same larval habitat. A competitive displacement of *Ae. aegypti* by *Ae. albopictus* has been well documented, especially in North America (Hobbs et al. 1991, O'Meara et al. 1995, Lounibos et al. 2002). In Mayotte, *Ae. albopictus* distribution range has extended rapidly. Indeed, *Ae. albopictus* and *Ae. aegypti* often co-occurred in the same habitats (in >37%), suggesting that these species overlap considerably in habitat use and

could encounter one another frequently as larvae. Therefore, biotic interactions between these two species like interspecific competition might also explain the observed distribution for both *Aedes* species after *Ae. albopictus* invasion, and laboratory studies are needed to test this hypothesis. Mayotte constitutes a very interesting study area where long-term surveillance should be carried out to follow the evolution of the situation between these two species.

Aedes aegypti, recorded as the vector of dengue epidemics that occurred in Mayotte in 1943 (McCarthy and Brent 1943), is common in anthropogenic areas during the rainy season and must still be considered important in terms of public health. However, particular attention must be paid to *Ae. albopictus*, which is now widespread in Mayotte, with a distribution closely related to human population concentrations, whatever the season. Its presence in the island is obviously a major concern for public health, increasing the risk of both the introduction and further transmission of arboviruses (Gubler 2003). The importance of *Ae. albopictus* as an epidemic vector of human pathogens has rarely been shown out of its area of origin and its presence may modify indigenous arboviruses transmission. This species has been the major vector, perhaps the only one, for the transmission of Chikungunya virus in Italy (Beltrame et al. 2007), in Central Africa, in Réunion Island, in Mauritius, and probably in Madagascar (Reiter et al. 2006, Schuffenecker et al. 2006). It has likely been largely implicated in the Chikungunya epidemics observed in Mayotte in 2005–2006, at least for the cases that arose in urban and suburban areas, where *Ae. albopictus* is the dominant species. The only known strategy for reducing arboviruses transmission aims at reducing vector populations, which is achieved through interventions in the most productive water containers. The measure of efficiency determined the relative contribution of a container type to mosquitoes density taking into account the number of pupae produced and the frequency of the container. For *Ae. aegypti*, pots and barrels produced >55% of total pupae collected, and for *Ae. albopictus*, barrels and buckets produced >60% of total pupae collected. Therefore, mechanic control of these larval habitats (i.e., covering or draining them) might be the most appropriate vector control measures. Such a strategy requires strong community participation of the local population in vector controls by increasing communication and sanitary education. Conversely, the control of *Ae. aegypti*, which develops mainly in natural larval habitats on the island, might be more difficult.

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