

## NATURAL HABITATS OF *Aedes aegypti* IN THE CARIBBEAN— A REVIEW

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**ABSTRACT.** Natural breeding habitats of *Aedes aegypti* in the Caribbean region were reviewed by conducting larval surveys in Trinidad, Puerto Rico, and the U.S. Virgin Islands and referring to records from the Mosquitoes of Middle America project. Twelve types of natural habitats were recorded: rock holes (9.7%), calabashes (2.4%), tree holes (19.5%), leaf axils (4.8%), bamboo joints (14.9%), papaya stumps (7.3%), coconut shells (4.8%), bromeliads (7.3%), ground pools (14.9%), coral rock holes (9.7%), crab holes (2.4%), and conch shells (7.3%), of which the coconut shell and calabash habitats were new to the Caribbean. The countries having the highest prevalence of natural habitats were Trinidad, Puerto Rico, and Jamaica, with 9 types (22.0%), 7 types (17.0%), and 6 types (14.6%), respectively. The distribution of natural habitats of *Ae. aegypti* in the Caribbean region is discussed in relation to vector control measures.

**KEY WORDS** *Aedes aegypti*, natural habitats, breeding sites, new records, review, Caribbean

### INTRODUCTION

The origin of *Aedes aegypti* (Linn.) is deeply rooted in Africa where 3 taxa are recognized: *Aedes aegypti* s.s. (type form), *Ae. aegypti formosus* (Walker), and *Ae. aegypti queenslandensis* (Theobald) (Mattingly 1957). The geographic spread of *Ae. aegypti* to the Caribbean region from Africa occurred during the slave trade in the 16th and 17th century when ships also introduced breeding populations of these mosquitoes (Pico 1969). The *Ae. aegypti* populations transported to the Caribbean belonged to the type form, a highly domesticated species inhabiting artificial containers used for storing clean water (Soper 1952, Trapido and Galindo 1956, Monath 1994). In contrast, subspecies *formosus* is confined to Africa south of the Sahara and larvae occur in natural tree hole habitats. Subspecies *queenslandensis* is distributed in the Mediterranean area, India, and Australia and breeds in artificial containers (Mattingly 1957).

In the Caribbean basin, larvae of *Ae. aegypti* occupy artificial containers such as gutter eaves in Suriname (Tinker 1974), and drums, tubs, buckets, and cisterns in Puerto Rico (Moore et al. 1978), the Cayman Islands (Nathan and Giglioli 1982), Antigua (Giglioli 1979), Trinidad (Chadee 1984, 1992), and Tobago (Chadee 1990). The main natural habitats of *Ae. aegypti* are tree holes (Clare 1915, Kellest and Omardeen 1957), bromeliads (MacDonald 1917, Moore 1983), papaya stumps (Laird and Mokry 1983), and rock holes (MacDonald 1917, Cook 1931, Fox et al. 1960, Nathan and Giglioli 1982, Moore 1983, Parker et al. 1983).

The use of both natural and artificial habitats suggests that *Ae. aegypti* may have undergone behavioral changes due to pressure from insecticide

use (Tinker 1974) and the widespread removal of containers in the domestic and peridomestic environment (Moore 1983, Chadee 1991). McClelland (1967) suggested that vector control measures might eliminate panmictic breeding, and thus lead to inbreeding among the limited surviving populations, which would enhance rapid evolutionary changes.

During the course of the *Ae. aegypti* eradication program in Trinidad (1976-91), which involved routine house inspection and treatment of both natural and artificial breeding containers, numerous larval habitats were encountered. In addition, during 1984 a similar survey was conducted in Puerto Rico and U.S. Virgin Islands to determine the occurrence of *Ae. aegypti* in natural containers. In this paper we review the natural habitats used by *Ae. aegypti* in the Caribbean, including 2 newly identified larval habitats.

### MATERIALS AND METHODS

In Trinidad from January 1981 to December 1991, all houses and compounds containing potential *Ae. aegypti* breeding sites were inspected by workers from the Insect Vector Control Division (IVCD) using the Pan American Health Organization (PAHO) guidelines (PAHO 1968). All natural and artificial containers were inspected. Immature *Ae. aegypti* were collected and placed into vials, labeled, recorded on standard forms, and sent to the IVCD laboratory, Ministry of Health, St. Joseph, Trinidad, where immatures were identified by one of us (D.D.C.). Tree holes and bromeliads above 1.8 m were not inspected due to a lack of ladders and other service equipment.

The collection records of J. M. Belkin at the Smithsonian Institution, Washington, DC, were reviewed and checked using the publications of Belkin and Heinemann (1973, 1975a, 1975b, 1976a, 1976b, 1976c) to determine whether *Ae. aegypti* had been found in husks or shells of fruits such as the calabash (*Crescentia cujete* Linn.) and coconut

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Table 1. Numbers of *Aedes aegypti* larvae collected from natural habitats in Trinidad, West Indies (1981-91).

Year	Natural habitats <sup>1</sup>									Total
	RH	CB	TR	LA	BA	PA	CS	BR	GP	
1981	10	97	24	11	6	5	14	3	2	172
1982	12	29	53	24	9	0	0	0	0	127
1983	8	8	29	8	5	7	2	5	1	73
1984	10	35	40	14	7	4	12	4	2	128
1985	12	53	31	21	7	5	19	3	1	152
1986	14	41	53	13	18	7	10	3	1	160
1987	8	81	56	19	3	3	11	9	0	190
1988	10	23	37	26	13	14	13	7	2	145
1989	9	62	29	32	9	11	21	4	0	177
1990	7	29	44	15	5	7	26	9	1	143
1991	14	69	28	19	11	8	14	7	4	174
Total	114	527	424	202	93	71	142	54	14	1,641

<sup>1</sup> RH, rock hole; CB, calabash; TR, tree hole; LA, leaf axil; BA, bamboo joint; PA, papaya stump; CS, coconut shell; BR, bromeliad; GP, ground pool.

(*Cocos nucifera* Linn.) in the Caribbean. The following Caribbean islands were checked: Anguilla, Antigua, Bahama Islands, Barbados, Barbuda, Cayman Islands, Dominican Republic, Guadeloupe, Grenada, the Grenadines, Haiti, Jamaica, Martinique, Montserrat, Nevis, Puerto Rico, St. Kitts, St. Lucia, Trinidad, and the Virgin Islands.

In addition, during 1984 *Ae. aegypti* were collected from natural containers in Puerto Rico and on 3 of the U.S. Virgin Islands using a similar methodology to that described by Moore (1983) and the Belkin files. The contents of all containers were removed and passed through a 100- $\mu$ m-mesh screen. Fourth-instar larvae were identified, whereas 1st to 3rd instars were reared to either the 4th instar or the adult stage for identification.

## RESULTS

Table 1 shows the natural habitats of *Ae. aegypti* encountered from routine house inspections in Trinidad from 1981 to 1991. A total of 1,641 *Ae. aegypti* larvae were collected from 9 types of natural habitats. The most frequently used natural sites were calabash fruits (32.1%) and tree holes (25.8%). The calabash collections may represent the first record of *Ae. aegypti* from such habitats in the Caribbean region (Figs. 1A, 1B). Rock hole-breeding *Ae. aegypti* were also recovered from sites in Port of Spain, Trinidad, and Gaspar Grande (an island off Trinidad). Coconut shells (husks) harbored *Ae. aegypti* in Trinidad but the prevalence was low (8.7% or 142 larvae). This also represents the first record of *Ae. aegypti* from coconut shell habitats in the Caribbean region (Figs. 1C, 1D). Larval *Ae. aegypti* were also collected from papaya stumps, bromeliads, bamboo stands, and leaf axils but the numbers recorded were small, 4.3% (71), 3.3% (54), 5.7% (93), and 12.3% (202), respectively.

Table 2 shows the distribution of *Ae. aegypti* in natural habitats by counties in Trinidad. St. George

contained 8 out of the 9 natural breeding habitats recorded for Trinidad, with the 2nd largest number of habitats found in St. Patrick and St. David. Coconut shells were observed in St. George and Caroni but the incidence of usage by *Ae. aegypti* was generally low. In St. George, St. David, and St. Patrick bromeliads frequently harbored immature *Ae. aegypti*. In St. Patrick, a single collection of *Ae. aegypti* larvae was made from the bromeliad *Aechmea nudicaulis* Linn., which is a very common epiphyte (Pittendrigh 1950). In St. George and St. David, larvae were collected from the bromeliads *Tillandsia fasciculata* Swartz and other *Tillandsia* species.

Table 3 shows the natural habitats of *Ae. aegypti* found in the Caribbean Basin. The search at the Smithsonian Institution disclosed no records of *Ae. aegypti* from calabash and coconut shell habitats in the Caribbean, thus, making use of these 2 habitats by *Ae. aegypti* a new discovery. Three islands, Trinidad, Puerto Rico, and Jamaica, accounted for almost 55% of all the atypical habitats encountered by us and those found by Belkin and Heinemann (1973, 1975a, 1975b, 1976a, 1976b, 1976c). Tree holes (8 or 19%), bamboo joints (5 or 11.9%), coral rock holes (4 or 9.5%), and rock holes (4 or 9.5%) were the major atypical breeding habitats of *Ae. aegypti* in the Caribbean region. These 4 sites constitute 50% of the breeding found in natural habitats.

Seven natural habitats were identified in Puerto Rico and 5 were identified in the U.S. Virgin Islands. In Puerto Rico, tree holes found harboring *Ae. aegypti* were located in Arecibo (Municipio de Arecibo), Bayamon (Parsella Juan Sanchez), Lajes (Municipio de San German), and Rio Grande (area south of Palmer to El Yungue Natural Forest). From the U.S. Virgin Islands, collections from tree holes were made at Cinnamon Bay Campground in St. John and at Fredrickstad in St. Croix. The main associated species was *Aedes mediovitatus* (Co-



Fig 1. A. Calabash tree (*Crescentia cujete* Linn.) with fruit. B. Calabash being used in a orisha temple. C. Coconut palm (*Cocos nucifera* Linn.) with fruit. D. Coconut shell as a suitable *Aedes aegypti* (Linn.) habitat.

Table 2. Distribution of natural breeding habitats of *Aedes aegypti* by counties in Trinidad, West Indies.

County	Natural habitats <sup>1</sup>									No. habitat types
	RH	CB	TR	LA	BA	PA	CS	BR	GP	
St. Andrew		x								1
St. David		x	x	x	x			x		5
St. George	x	x	x	x		x	x	x	x	8
St. Patrick		x	x		x	x		x		5
Caroni							x			1
Nariva		x			x					2
Victoria		x				x				2
No. sites with habitat	1	6	3	2	3	3	2	3	1	24

<sup>1</sup> RH, rock hole; CB, calabash; TR, tree hole; LA, leaf axil; BA, bamboo joint; PA, papaya stump; CS, coconut shell; BR, bromeliad; GP, ground pool.

Table 3. Summary of the geographic distribution of natural habitats used by *Aedes aegypti* in the Caribbean Basin.

Site	Natural habitats <sup>1</sup>												No. habitat types
	RH	CB	TR	LA	BA	PA	CS	BR	GP	CR	CH	CO	
Anguilla <sup>2</sup>											x		1
Antigua <sup>2</sup>			x	x									2
Bahamas <sup>2</sup>									x				1
Barbados													0
Cayman Island	x												1
Dominican Republic <sup>2</sup>			x								x		2
Guadeloupe <sup>2</sup>					x				x				2
Grenada and the Grenadines								x					1
Haiti <sup>2</sup>			x								x		2
Jamaica <sup>2</sup>	x		x	x					x	x	x		6
Martinique <sup>2</sup>					x				x				2
Montserrat													0
Nevis													0
Puerto Rico	x		x		x	x	x	x				x	7
St. Kitts <sup>2</sup>			x										1
St. Lucia													0
Trinidad	x	x	x		x	x	x	x	x			x	9
U.S. Virgin Islands			x		x	x						x	4
No. sites with habitat	4	1	8	2	5	3	2	3	5	4	1	3	41

<sup>1</sup> RH, rock hole; CB, calabash; TR, tree hole; LA, leaf axil; BA, bamboo joint; PA, papaya stump; CS, coconut shell; BR, bromeliad; GP, ground pool; CR, coral rock hole; CH, crab hole; CO, conch shell.

<sup>2</sup> From Belkin and Heinemann collection records (1973, 1975a, 1975b, 1976a, 1976b, 1976c).

quillet). Papaya stumps were infested with *Ae. aegypti* and *Ae. mediovittatus* at Arecibo and Rio Grande in Puerto Rico and at the Village of Old Tutu on St. Thomas in the U.S. Virgin Islands. *Aedes aegypti* was also collected from bamboo stands at Rio Grande, Aibonito, and San Juan, Puerto Rico. Similar collections in bamboo stands were made at the Village of Old Tutu and at Fredrickstad in St. Thomas and St. Croix, respectively.

In Puerto Rico bromeliads contained immature *Ae. aegypti* at Bravos de Boston in San Juan, at Barrio Florecio and Barrio Clarita in Fajardo, at Reparto Teresita and Parsella Juan Sanchez in Bayamon, and at Barrio Villa Nueva in Caquas. *Wyeomyia* sp. and *Ae. mediovittatus* were species associated with *Ae. aegypti* in the bromeliads. No immature *Ae. aegypti* were found in bromeliads in the U.S. Virgin Islands.

Coconut husks (shells) served as larval habitats for *Ae. aegypti* in Puerto Rico. Collections were made at Parsellas Juan Sanchez and Parsellas Rio Plantation in Bayamon. *Aedes mediovittatus* also shared this habitat. This collection also represents a first record of *Ae. aegypti* using this habitat in the Caribbean. Conch shells were also utilized by gravid *Ae. aegypti* as suitable oviposition sites and immatures were collected at Parsellas Juan Sanchez in Bayamon and at Los Corabis and Sardinera in Fajardo, Puerto Rico. A coral rock hole with *Ae. aegypti* immatures was also found in Palmas Altas in Carceloneta, Puerto Rico.

## DISCUSSION

Coconut shells and calabashes were 2 newly encountered *Ae. aegypti* larval habitats. Coconut

shells were found in both Puerto Rico and Trinidad, whereas the calabash habitat was found only in Trinidad (Fig. 1). The prevalence of *Ae. aegypti* immatures was quite low in coconut shells (8.7% or 142). One obstacle to greater utility of the coconut habitat may be that the water becomes heavily organic as the epicarp or fragments of the nut decay. Although the coconut shell represents a new habitat for the Caribbean region, this is a common *Ae. aegypti* habitat in Africa and in the Pacific islands (Christophers 1960), as well as in southeast Asia (Macdonald 1956).

Christophers (1960) found breeding by *Ae. aegypti* in calabashes to be almost universal in African native huts. In Trinidad, the recent resurgence of the orisha faith (a religion brought to the Caribbean during the slavery years, 1501–1830), has increased the use of calabashes for religious ceremonies or rituals, thus providing *Ae. aegypti* with an additional breeding site (Table 1). These calabashes are used as flower vases with clean water; the flowers are changed regularly in homage to the gods. As many as 8 calabashes can be found in homes or churches of orisha followers (Fig. 1B). Often the orisha priest objects to the calabashes being treated with insecticides. This has instilled fear among vector control workers who sometimes refuse to inspect and treat these premises. Consequently, these untreated calabashes with *Ae. aegypti* immatures can reinfest surrounding houses and later the community. Therefore, a concerted effort to educate the communities and the vector control workers could be used to alter attitudes and behavior, resulting in a reduction in mosquito indices.

The bromeliad habitat of *Ae. aegypti* has been reported in Grenada (MacDonald 1917), Puerto Rico (Moore 1983), and in Trinidad (present study). Bromeliad-inhabiting mosquitoes are difficult to control because the arrangement of the leaves of bromeliads in an upright tube protects the interfoliar water from insecticide application (Pittendrigh 1950). In Trinidad, *Ae. aegypti* were collected from both dried calabashes (at ground level) and in bromeliads from calabash trees.

Tree holes are probably the type habitat of *Ae. aegypti* in Africa (Hopkins 1952). Mattingly (1957) suggested the evolution of use of various breeding habitats by *Ae. aegypti* started with the utilization of exposed rock holes, then shaded rock holes, then horizontal, fallen trees, and finally holes in vertical, standing trees. Clare (1915) first reported *Ae. aegypti* breeding in tree holes and in bamboo joints in Trinidad and possibly the Caribbean region. Kellert and Omardeen (1957) found significant numbers of *Ae. aegypti* occupying tree holes from ground level to 10.4 m. Our study suggests that very little has changed in the preference of *Ae. aegypti* for tree hole habitats. In addition, *Ae. aegypti* has been reported in papaya stumps in Tuvalu and Suriname (Laird and Mokry 1983). Similar collections from papaya stumps were made in Trinidad and Puerto Rico but the incidence was low. Despite the early collections of *Ae. aegypti* from bromeliads in Grenada (MacDonald 1917) and from rock holes in Haiti (Cook 1931), Soper (1952) and Trapido and Galindo (1956) reported the almost exclusive urban breeding of *Ae. aegypti* in artificial containers in and around houses.

The current literature indicates numerous cases of *Ae. aegypti* breeding in rock holes in the Caribbean, as demonstrated in Haiti (Cook 1931), Puerto Rico (Fox et al. 1960), Jamaica (Belkin et al. 1970), Cayman Brac (Nathan and Giglioli 1982), and Anguilla (Parker et al. 1983). Rock hole breeding was observed at Port of Spain, Trinidad, and on Gaspar Grande, an island located off the northwestern peninsula of Trinidad (Chadee et al. 1985).

The use of natural containers by *Ae. aegypti* in both domestic and semiwild conditions supports the view that the type form *sensu stricto* was transported to the Caribbean during the 16th and 17th centuries (Mattingly 1957). Thus, *Ae. aegypti* populations had more than 400 years to evolve optimal container preferences. The present occurrence of *Ae. aegypti* in natural breeding habitats within the Caribbean region and the abundant collections of *Ae. aegypti* s.s. from coral rock holes on Anguilla (Parker et al. 1983) suggest that despite the number of generations since the introduction of *Ae. aegypti* into the Caribbean, a strong selective pressure to change breeding sites from natural to artificial did not occur, but that the species retained the ability to use both types of sites. Schoof (1959) suggested the possible elimination of the domestic component of the *Ae. aegypti* populations by insecticide appli-

cation. He envisaged that this procedure would leave only the feral portion of the population that occupies natural habitats to become the dominant strain. Based on our study and that of others (Focks et al. 1981, Chadee 1984), feral attributes evidently have not become dominant among the *Ae. aegypti* populations but neither have these attributes been lost. A mitigating factor restricting the expected behavioral change may be related to pressure from insecticide use and the source reduction campaigns conducted during the last 2 decades. These campaigns may have counteracted any selection for only one option, that is, either artificial or natural habitats. On the other hand, Wynne-Edwards's (1962) concept of an epideictic phenomenon may apply to the reduction of egg laying due to the interaction between females at high densities at oviposition sites, which at the same time may promote further searching for suitable oviposition sites and the utilization of a wider range of sites.

Wallis et al. (1984) showed gene frequency patchiness among Caribbean populations of *Ae. aegypti* and some collections did not conform to any geographic pattern. These results suggest that high migration rates among the islands and the mainland can introduce fresh genetic material, which may affect vector competence, insecticide resistance, and ecological adaptation. Therefore, numerous factors may account for the retention of oviposition preferences for both natural and artificial habitats. For example, the use of both artificial and natural breeding sites by *Ae. aegypti* may reduce intraspecific competition (Shannon and Putnam 1934, Mulla 1979) and not decrease the fecundity of individuals (Begon and Mortimer 1986), but increase the number of optimal breeding sites available (Moore 1983, Chadee 1987), reduce competition for a limited resource (Begon and Mortimer 1986, Chadee 1993), and reduce density-dependent factors (Terzian and Stahler 1949, Moore and Fisher 1969, Gilpin and McClelland 1979). Consequently, *Ae. aegypti* populations that can switch oviposition preferences from natural to artificial containers and vice versa would increase fitness by reducing search time, time-dependent mortality, and competition (Moore and Fisher 1969, Hassell 1978, Begon and Mortimer 1986, Chadee 1993). This very complex situation may explain why past efforts at eradication of *Ae. aegypti* have had limited success.

Recognition of the contribution of natural breeding sites to maintenance of populations of *Ae. aegypti* is an essential component in the abatement of dengue and other pathogens transmitted by this species. These habitats, when found in close proximity to houses, are generally overlooked by abatement personnel and could provide a source of mosquito vectors as well as a harborage for posttreatment infestations. Moreover, in feral and peridomestic habitats, sharing of natural habitats with other mosquito species, such as *Ae. mediovittatus* in Puerto Rico, could play a key role in the long-term persistence

of the dengue viruses during interepidemic periods, as reported by Gubler et al. (1985).

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