Characterization of *Anopheles darlingi* (Diptera: Culicidae) Larval Habitats in Belize, Central America

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ABSTRACT Surveys for larvae of *Anopheles darlingi* Root were conducted in April, May, and August 1994 in riverine habitats of central Belize (Cayo and Belize districts). *An. darlingi* was present during both the dry and wet seasons. Larvae were encountered most frequently in patches of floating debris along river margins. The floating mats were often formed by bamboo hanging over the banks and dense submersed bamboo roots. Larvae were found less frequently in lake margins, small lagoons, and ground pools with submersed roots and patches of floating leaves or vegetation. In addition to their association with floating debris, larvae of *An. darlingi* were associated positively with shade and submersed plants in riverine environments. Samples from river habitats showed the larvae of *Anopheles albimanus* Wiedemann to be strongly associated with sun-exposed sites containing green or blue-green algae. Unlike *An. darlingi, An. albimanus* was an ubiquitous mosquito, the immatures of which occurred in a wide variety of riverine and nonriverine aquatic habitats. Based on published reports and our experience, the association of *An. darlingi* with river systems was verified, and its distribution in Central America and Mexico was mapped.

KEY WORDS *Anopheles darlingi, Anopheles albimanus,* larval habitats, malaria vectors, distribution, Belize

Anopheles darlingi Root is distributed discontinuously from southern Mexico to southern South America with a gap from Nicaragua, Costa Rica to Panama where the species has not been officially reported (Komp 1940; Kumm and Ram 1941; Kumm et al. 1943; Vargas and Palacios 1955, 1956; Linthicum 1988; Rivera Nuñez 1990). *An. darlingi* appears to be an important vector of human malaria throughout its geographic range (Deane et al. 1946, Foote and Cook 1959, Arruda et al. 1986, Fleming 1986, Klein et al. 1991). Despite its medical importance, our knowledge of the larval ecology of *An. darlingi* is remarkably limited. In fact, there are no published systematic studies of *An. darlingi* larval ecology from southern Mexico or northern Central America. Even for South America, there are relatively few published observations on the larval ecology of this important vector (Root 1926; Shannon 1931; Barreto 1938; Pinto 1939; Stage and Giglioli 1947; Faran and Linthicum 1981; Rozendaal 1990, 1992).

The few reports of *An. darlingi* ecology have been consistent in mentioning that larvae were found in shaded or partly shaded mats of floating debris or floating vegetation in areas inundated by rivers and streams (Root 1926; Barreto 1938; Komp 1941; Kumm and Ram 1941; Faran and Linthicum 1981; Rozendaal 1990, 1992). In Belize, larvae of *An. darlingi* have been collected in roots, floating debris, or vegetation along shaded margins of slowly running streams and, until our recent studies, their presence was last reported in the 1940s (Komp 1940, Kumm and Ram 1941).

Through captures of anophelines landing on humans around houses in central Belize, we documented the presence of *An. darlingi* for the 1st time in almost 50 yr (Harbach et al. 1993, Roberts et al. 1993). However, during 3 previous years of extensive larval collections throughout Belize, no immature stages of *An. darlingi* were encountered (Rejmankova et al. 1993, Roberts et al. 1993). For the current study, collection effort was directed specifically at *An. darlingi* larval habitats in central Belize. Clues about natural *An. darlingi* larval habitats extracted from the literature and our field work (Harbach et al. 1993) indicated that *An. darlingi* larvae should be found in shaded mats of floating debris or vegetation along margins of rivers or streams. Our goal was to test this hypothesis and to define other variables associated with the presence of *An. darlingi* larvae. Because there is no composite picture of *An. darlingi* distribution in

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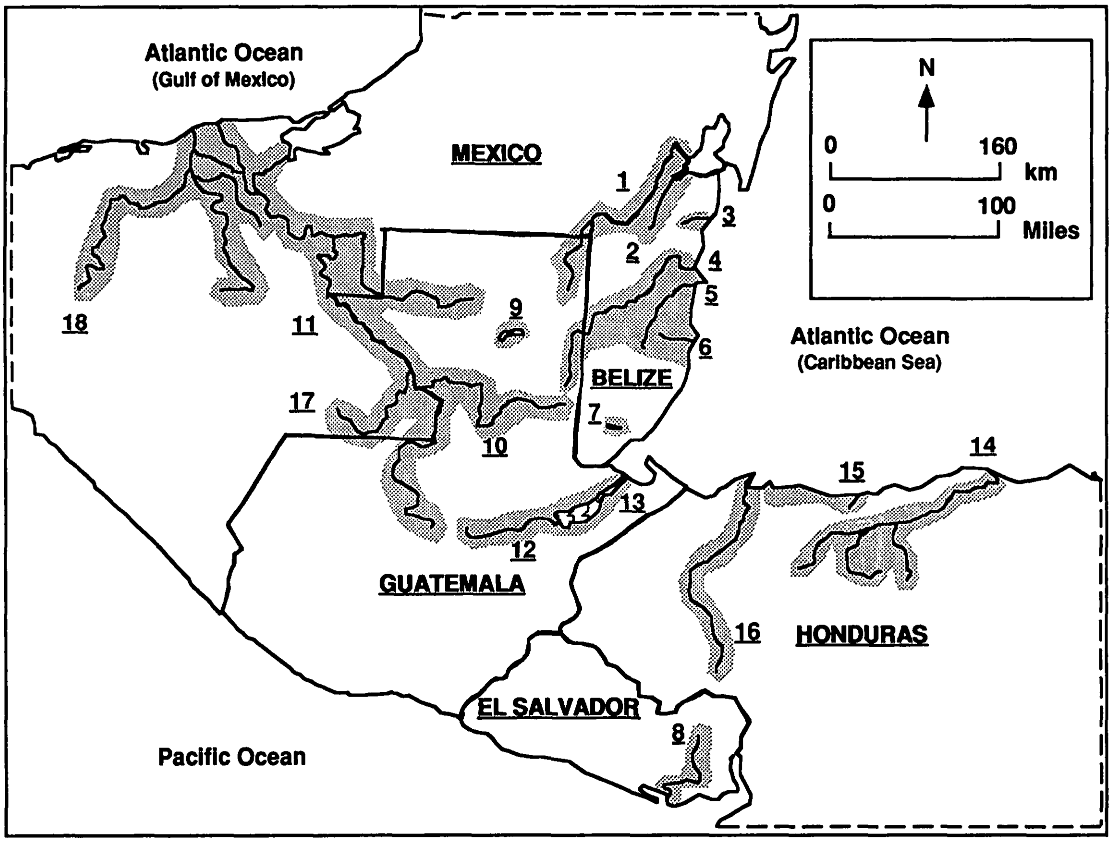

Fig. 1. Geographic distribution (shaded river systems) of *An. darlingi* in Central America and Mexico based on the references cited in Table 2. Numbers refer to different river systems listed in Table 2.

Mexico and Central America, a list of published records and a map of river systems delineating the northern distribution of this important malaria vector are included in the discussion section (Fig. 1).

Materials and Methods

Study Area. The study area (Fig. 1, river systems 4–5; Table 2) is located in Central America between the karstic foothills and the Caribbean Sea in central Belize (Cayo and Belize Districts).

Table 1. Variables significantly associated with the presence or absence of *An. darlingi* or *An. albimanus* larvae in the dry season of 1994 (n = 30 collections)

Variable	Chi-square[a]	
Habitat with floating debris	*An. darlingi*	*An. albimanus*
Shaded	5.12*	1.77
Submersed vegetation	3.94*	1.12
Presence of algae[b]	3.31	7.54**
Depth < 0.5 m	0.52	0.02

[a] **, $P < 0.01$; *, $P < 0.05$; or nonsignificant, $P > 0.05$. df = 1 for each comparison; significant pairs were associated positively.
[b] Green or blue-green algae.

Annual rainfall is ≈2,400 mm in the Belize City area with a wet season from May to December. The growth of citrus plantations and secondary forests close to creeks and rivers is typical for this region. The malaria rates of Cayo and Belize Districts represented 40% of all cases in Belize in 1993, with 87% of these 2,139 cases occurring in the Cayo District (Ministry of Health 1993).

Specific collecting sites were located along the Belize River system including Belize River and Mussel Creek; and the Sibun River system including Sibun River, Nancy Porter Creek, Dry Creek, and other small tributaries (creeks, oxbows), and Five Blues Lake.

Mosquito Collections. Guided by 3 yr of extensive larval surveillance throughout Belize, adult collections that documented the presence of *An. darlingi* along the Sibun and Belize river systems (Harbach et al. 1993, Roberts et al. 1993), and the 2 old reports on *An. darlingi* larval habitats in Belize (Komp 1940, Kumm and Ram 1941), we targeted the margins of the Sibun and Belize rivers for *An. darlingi* larval collections. Earlier results indicated that *An. darlingi* larvae were present in habitats with a concentration of floating debris (pieces of wood, dead leaves, flowers, and seeds)

Table 2. Known distribution of *An. darlingi* in Central America and Mexico

Country	District	Location[a]	River system	References
Belize	Corozal	Chan Chen	1 Rio Hondo	Present work
	Corozal–Orange Walk	Libertad, San Estevan	2 New River	Present work
	Belize	Maskall	3 Northern River	Present work
	Cayo–Belize	Burrell Boom	4 Mussel Ck (Belize River)	Present work
		Bridge, Hershey, Galvez	5 Sibun River	Present work
		Churchyard, La Democracia	5 Nancy Porter Ck (Sibun River)	Present work
		Five Blues Lake	5 Indian Ck (Sibun River)	Present work
	Stann Creek	Silk Grass, Dog Ck	6 Silk Grass Ck	Komp 1941
		Agricultural station Quarry, 23 Miles	6 Northern Stann Ck	Kumm and Ram 1941
	Toledo	Farmer's Grade, quarry		Kumm and Ram 1941
		Trosa	7 Trosa Ck	Kumm and Ram 1941
El Salvador	San Miguel	20 km east Laguna El Jocotal	8 Rio Grande de San Miguel	Pecor, pers. comm.*
Guatemala	Petén	Cimarron	9 Lago Petén Itzà	Kumm et al. 1943
		Sayaxché	10 Rio de la Pasión	Kumm et al. 1943
		Santa Teresa	10 Rio El Subin (Rio de la Pasión)	Kumm et al. 1943
		El Desempeño	11 Rio Usumacinta	Kumm et al. 1943
	Alta Verapaz	Panzos	12 Rio Polochic	Komp 1941
	Izabal	Km. 264.5, at Finca El Milagro	13 Rio San Marcos	Clark-Gil and Darsie 1983
Honduras	Yoro & Colón	Valle del Aguán	14 Rio Aguán	Lacey et al. 1986
	Atlántida	Sinai	14 Rio Aguán	Rivera Nuñez 1990
		La Ceiba	15 Rio Cangrejal	Rivera Nuñez 1990
		Esparta	15 Rio San Juan	Rivera Nuñez 1983
		Km 17	15 Rio Leán	Komp 1941
		Tela	15 Rio Leán	Rivera Nuñez 1990
	Santa Barbara	Santa Barbara	16 Rio Cececapa (Rio Otoro/Uluá)	Rivera Nuñez 1990
Mexico	Chiapas	Anaite	11 Rio Usumacinta	Kumm et al. 1943
		In Lacandon Forest, Chajul, Reforma	17 Lacantún River (Rio Usumacinta)	Loyola et al. 1991
	Tabasco	Macuspana (Aquiles Serdán, Benito Juárez, Macuspana)	18 Rio Puxcatán (Rio Grijalva)	Vargas and Palacios 1955
		Paraiso (Puerto Ceiba)	18 Rio Seco (Rio Grijalva)	Vargas and Palacios 1955
		Tacotalpa (Tacotalpa, Tapijulapa)	18 Rio Tacotalpa (Rio Grijalva)	Vargas and Palacios 1955
		Teapa	18 Rio Teapa (Rio Grijalva)	Vargas and Palacios 1955

[a] Name of major river system in parentheses; Ck, creek. For location, see Fig. 1.
[b] Collected by J. R. Austin on 22 September 1965; voucher specimen in the Smithsonian Institution, Washington, DC.

or aquatic plants such as *Cabomba* sp. (Harbach et al. 1993). Therefore, we focused our sampling effort on these potential habitats.

The survey was conducted during the dry season of April and May 1994, with additional samples collected during the wet season in August 1994. Larval collections were made from a inflatable raft to sample deep-water habitats on both sides of the river. The longitude and latitude of each habitat was recorded with a geographic positioning system (Ensign GPS) to allow us to georeference the larval data into a geographic information system being developed for the national malaria vector control program of Belize. For all *Anopheles*-positive habitats, we recorded the type of larval habitat, water current, depth, vegetation (submersed, floating, emergent), and algae (green, blue-green, filamentous). The aquatic plants were sampled and identified in the laboratory, and pH and conductivity were measured in situ with portable meters.

At each larval habitat, a minimum of 10 dips for anopheline mosquitoes was taken. The captured immatures were reared individually in vials and fed baby fish food until pupation and adult emergence. Adults were identified to species using Wilkerson et al. (1990), and associated larval and pupal skins were preserved. Taxonomic voucher specimens have been deposited at the Walter Reed Biosystematics Unit of the Smithsonian Institution, Washington, DC.

Results

During the dry-season survey, *Anopheles* adults were reared from 30 of 33 positive larval collections from potential *An. darlingi* larval habitats. Among these, larvae of *An. darlingi* were present in 20 habitats (67%), *An. albimanus* Wiedemann in 20 habitats (67%), and *An. pseudopunctipennis* Theobald in 6 habitats (20%). Larvae of *An. darlingi* and *An. albimanus* were found jointly in 11 habitats (55%). *An. pseudopunctipennis* larvae occurred in 1 habitat with *An. darlingi* larvae and in 4 habitats with *An. albimanus* larvae. *An. darlingi* and *An. albimanus* were collected with *pseudopunctipennis* 1 and 4 times, respectively, and all 3 species were found together only once. No significant positive or negative interspecific associations were found between *An. darlingi*, *An. albimanus*, and *pseudopunctipennis* using Cole's index (1949), as modified by Hurlbert (1969) for paired species.

A drought during the early 1994 wet season resulted in a drastic reduction of potential larval habitats. Of the 10 positive habitats found in August 1994, larvae of *An. darlingi* were present in 6 collections (60%), *An. albimanus* in 7 (70%), and *pseudopunctipennis* in 1 (10%). Larvae of *An. darlingi* and *An. albimanus* occurred together in 4 habitats.

The key determinant for presence of *An. darlingi* larvae was the presence of floating mats of wood pieces, dead leaves, and flower and seed debris. Additionally, chi-square analyses were conducted for the presence or absence of *An. darlingi* or *An. albimanus* larvae in habitats with full sunlight versus shade–partial shade, with or without submersed plants, with or without algae, and different depths of water (Table 1). Shaded–partly shaded habitats and submersed plants such as *Cabomba* sp. were 2 factors that were significantly ($P < 0.05$) associated with *An. darlingi* larvae. The presence of green or blue-green algae was a determining factor ($P < 0.01$) for the presence of *An. albimanus* larvae.

Overall, 75% of the habitats containing *An. darlingi* larvae were along river or stream margins. These habitats were frequently found in areas shaded by bamboo hanging over the banks, with floating mats being formed in the dense bamboo root system. Other habitats positive for *An. darlingi* larvae were lake margins (15%), small lagoons (5%), and ground pools (5%).

The pH values among all *Anopheles*-positive larval habitats ranged from 6.49 to 6.93. Water conductivity fluctuated within the range limits of fresh water to slightly brackish water, 70–260 μS (microSiemens) in the Sibun River system and 950–1220 μS in the Belize River system. There were no significant associations of pH and conductivity values with the presence of *An. darlingi* or *An. albimanus* larvae. Water depth varied from 0.1 to 2.0 m. Water current within mats of floating debris was either slow or undetectable. In contrast, a fast current characterized the water beneath the floating mats and beyond the physical barriers that caused the mats to form.

In northern and central Belize, adults and larvae of *An. darlingi* have been collected in all major lowland river systems (Fig. 1). The known distribution of *An. darlingi* with reference to the country, precise locations, and river systems is described in Table 2. In Guatemala, *An. darlingi* was reported along 3 lowland river systems and lakes of 3 states (Petén, Alta Verapaz, and Izabal). In Honduras, *An. darlingi* was collected mainly along the Atlantic Coast in the states of Yoro, Colón, and Atlántida. However, *An. darlingi* also were captured inland, along the Uluá River system in the Santa Barbara District. In Mexico, *An. darlingi* was reported in the states of Chiapas and Tabasco along the Usumacinta River system, which delineates the frontier with Guatemala, and also along the Grijalva River system. In Central America, El Salvador was the only country where *An. darlingi* was reported in a locality near the Pacific Ocean. Based on the literature and our collections, *An. darlingi* was present in 18 lowland river systems of Central America and Mexico.

Discussion

Our dry- and wet-season collections in central Belize proved that *An. darlingi* was present in the Sibun River system during both seasons. However, seasonal effects on the relative abundance of *An. darlingi* populations are still unknown. The main types of *An. darlingi* larval habitats along the Sibun River were defined as mats of floating debris or patches of submersed plants (*Cabomba* sp.) that are shaded or partly shaded, especially by bamboo hanging over the banks. Bamboo clumps were common, and their dense root systems impeded the water current and permitted mats of floating debris to form at the water surface. Floating debris also formed around submersed tree roots, emergent branches, and floating logs. Mats of floating debris were favorable larval habitats because they protected larvae from predators and accumulated in areas with reduced current velocity which apparently attracted ovipositing females. *An. darlingi* larvae also were collected less frequently in lake margins, small lagoons, and ground pools.

A sudden flood of the Sibun River in August 1994 provided valuable information on the influence of flooding on larval survival. A heavy rain on 22 August caused extensive flooding of the Sibun River valley, but by midday of 23 August, the river was back to a normal flow rate. In the wake of this flood, mats of flotsam were isolated at different heights in the trees and along the edges of the river system. Mats were composed of fine pieces of wood and leaves that stayed compact and moist. On 23 August, a small lagoon adjacent to the Sibun River was sampled for larvae. Many 3rd and 4th instars and pupae of *An. darlingi* and *An. albimanus* were collected from floating mats of debris. Before this observation, we did not know that the larvae could survive a major flood and simply settle back into their original habitats as the water receded. As an experiment, about ≈4 liters of debris that had been stranded on the bank were placed on the water surface between sticks to prevent drifting with the current. By dipping, 2 live anopheline larvae were captured from the debris. These observations showed that larvae followed the floating debris with the receding water level and that some inevitably became stranded and perished. However, these observations were true only for parts of the river system that partially were protected from strong current. With the example cited above, the larvae were collected from a side lagoon of the river, where all the surrounding vegetation remained erect as the flood waters receded. No observations have been made that characterize the fate of habitats and larvae within the main river channel under flood conditions.

Another common behavior of *An. darlingi* was observed within the floating debris; larvae were found to move onto the upper surface and partially adhere to small pieces of debris when the water surface was disturbed during dipping. Additionally, *An. darlingi* larvae were very difficult to locate within the floating mats of wood debris because of their similar coloration.

From the few reports on *An. darlingi* larval collections, larvae were consistently collected from mats of floating debris or floating vegetation and in shaded or partly shaded areas (Root 1926, Barreto 1938, Komp 1941, Kumm and Ram 1941, Faran and Linthicum 1981). In a survey of *An. darlingi* breeding habitats in Suriname, Rozendaal (1992) found that *An. darlingi* generally was associated with riverine habitats in areas that were inundated by rivers and streams, such as creeks with sunlit areas; river edges in partial shade, in patches of floating vegetation where water current is impeded; and pools formed in or near the riverbed, with partial shade and near the forest edge. The lack of published reports on the larval ecology of *An. darlingi*, such as that of Rozendaal (1992), reflects the difficulties in finding its larval habitats. For example, the presence of *An. darlingi* larvae was not recorded by our team during intensive larval surveys between 1990 and 1992 (Roberts et al. 1996). Deep water or dense vegetation (or both) along the river banks make the river habitats generally inaccessible by foot. Our use of a raft for collecting was key to finding the various habitats along both sides of the river.

Among our larval collections, *An. darlingi* and *An. albimanus* larvae frequently were found together, but no significant interspecific association was detected. As reported by Kumm and Ram (1941), *An. albimanus* was the most widely distributed anopheline in Belize. It is an opportunistic species that occurs in a wide variety of water bodies. Savage et al. (1990) and Rejmankova et al. (1991, 1993) found that *An. albimanus* larvae were associated positively with green or blue-green algae. In contrast to the ubiquity of *An. albimanus*, *An. darlingi* is restricted to river and creek environments with mats of floating debris, shaded or partly shaded, and submersed plants. *An. darlingi* larvae also were collected from water bodies that were associated with the river and were at the same water level as the river. These associated bodies of water were produced by ground water and flowing subterranean water of the hyporheic zone. The subterranean water flow of the hyporheic zone has boundaries represented by surface water above and true ground water below. Because the hyporheic water is moving slowly, these surface bodies of water are continually refreshed. In other words, these water bodies and other *An. darlingi* larval habitats are linked to the river, and *An. darlingi* may be characterized as a riverine mosquito.

Based on collections of larvae and adults, *An. darlingi* occurs during both dry and wet seasons and in all major lowland river systems that have been sampled in Belize, from Corozal to Toledo Districts (Fig. 1). In Central America and Mexico, *An. darlingi* historically has been found along 18 river systems (Fig. 1, Table 2) in the lowlands of 5 different countries: Mexico, Guatemala, Belize, El Salvador, and Honduras. Unless river environments in these countries have changed during the past 40 yr, this compilation reflects the known distribution of *An. darlingi* in Central America and

Mexico. Seventeen of the 18 river systems feed into the Atlantic Ocean. The exception is the Rio Grande de San Miguel in El Salvador, which flows into the Pacific Ocean (Fig. 1). To date, we have not collected *An. darlingi* closer than 11 km to the coast (that is, Maskall on the Northern River). Larvae of *An. darlingi* were found in fresh water in the Sibun River system to slightly brackish water in the Belize River system.

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