Anopheles albimanus (Diptera: Culicidae) and An Example of Larval Habitat Selec

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Environ. Entomol. 25(5): 1058-1067 (1996)

ABSTRACT Northern Belize has extensive herbaceous wetlands. Those dominated by sparse emergent macrophytes, rushes (Eleocharis spp.) and sawgrass (Cladium jamaicense Crantz), often develop floating mats of cyanobacteria (blue-green algae). These mats provide suitable habitat for larvae of the malaria transmitting mosquito Anopheles albimanus Wiedemann. Presence/absence of A. albimanus larvae and cyanobacterial mats was assessed in marshes located throughout northern Belize. Of the 21 marshes examined during the 1993 wet and 1994 dry seasons, cyanobacterial mats were found in 11, and A. albimanus larvae were detected in 9 of these 11 marshes. No A. albimanus larvae were found in marshes without evanobacterial mats. Mosquito larvae were collected along two 1,000 m long transects in both the wet season (August 1993) and the dry season (March 1994) to delineate larval distribution in marshes with cyanobacterial mats. A. albimanus larval densities in cyanobacterial mats were relatively high in both seasons: 2.8 and 2.3 larvae per dip in the wet and dry seasons, respectively, in Chan Chen marsh; and 0.8 and 1.02 larvae per dip in Buena Vista marsh. Numbers of larvae per dip did not significantly change with increasing distance from houses/pastures or margins of the marsh. A field experiment showed a strong preference of ovipositing A. albimanus for cyanobacterial mats. Higher temperatures and higher CO₂ emissions from cyanobacterial mats are possible ovipositional cues.

KEY WORDS Anopheles albimanus, cyanobacterial mats, larvae, oviposition

DISTRIBUTION OF A species may be determined by the behavior of individuals selecting their habitat. Despite its obvious importance, habitat selection is one of the most poorly understood ecological processes (Krebs 1994). Oviposition site selection has been recognized as a critical factor for both the survival and population dynamics of mosquitoes, and it has important implications for mosquito control (Bentley and Day 1989). Mosquito oviposition behavior in the laboratory is well documented, but laboratory studies may not reflect mosquito behavior in the field (Bates 1940, Bentley and Day 1989). However, few anopheline oviposition experiments have been conducted in the field (Orr and Resh 1992). Associations of larval stages with aquatic vegetation, specifically, correlations between larval densities and quantity of intersection lines (i.e., air-water-plant interfaces), have been documented more frequently (Hess and Hall 1943, Hall 1972, Balling and Resh 1984). Habitat selection by larvae was described by Walker et al. (1988) and Orr and Resh (1992). In this article we present field results on the habitat selection of

Anopheles albimanus Wiedemann throughout the Northern Coastal Plain of Belize.

Anopheles albimanus is a major vector of malaria in the humid coastal lowlands of Central America and northern South America, extending to the Paria Peninsula in Venezuela and into the Greater Antilles (Faran 1980). Because of the medical importance of the species, the literature on its life history is quite extensive. Larvae of A. albimanus have been reported from a wide variety of habitats, usually sunlit or partially shaded shallow waters, both fresh and brackish, with sparse vegetation. Detailed descriptions of larval habitats of A. albimanus on the Pacific coast of Mexico and El Salvador can be found in Breeland (1972), Breeland et al. (1974), Bailey et al. (1980, 1981a, b), Savage et al. (1990), Rejmánková et al. (1991, 1992), and Rodriguez et al. (1993). Less information is available for the Caribbean coast with the exception of Haiti (Taylor 1966) and Belize, where the larval habitats of A. albimanus were recently described by our research team (Rejmánková et al. 1993). The seasonal abundance and distribution of A. albimanus varies with the availability of larval habitats. Areas with a pronounced difference in the amount of rain during the year, such as the Pacific coast of Mexico, would generally have higher abundance of A. albimanus during the rainy season (Rodriguez et al. 1993), whereas in areas with extensive wetlands that stay permanently flooded, such as low-

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lands of Belize, the species is abundant throughout the year.

Belize (former British Honduras), located on the southeastern part of the Yucatan Peninsula, has a substantial part of its lowlands covered by herbaceous wetlands. According to our previous studies, A. albimanus in Belize is often positively associated with floating cyanobacterial mats (i.e., mats of blue-green algae with precipitated calcium carbonate [Rejmánková et al. 1993]). Extensive marshes, many of which stay completely or partially flooded throughout the year, often develop large areas of cyanobacterial mats. Of the three common types of marshes frequently occurring in the Coastal Plain regions, only those with low densities of emergent vegetation (either rushes, Eleocharis spp., or sawgrass, Cladium jamaicense Crantz) provide suitable conditions for growth of cyanobacterial mats. Dense cattail (Typha domingensis Persoon) marshes cause shading that limits algal growth. Formation of cyanobacterial mats is restricted to marshes with water containing relatively large concentrations of mineral salts, specifically calcium carbonate and calcium sulfate (Lewin 1962, Pentecost 1991). In our 1990-1991 survey, waters with algal mats contained significantly higher Ca⁺² concentrations than waters without mats (P < 0.001; E.R., unpublished data).

The understanding of larval population dynamics and estimates of their population density and distribution have been defined as important parameters for mosquito control (Ikemoto 1978; Service 1971, 1985; Stewart et al. 1983; Walker et al. 1988; Pitcairn et al. 1994). Service (1993) summarized papers dealing with larval density/distribution and concluded that reliable estimates of larval densities are inherently difficult and that better sampling procedures need to be developed. Most researchers studying larval distributions are concerned only with small to medium size aquatic habitats (one to several hectares) or, as in the case of rice fields, only with small areas of larger habitats (Chambers et al. 1979, Andis et al. 1983, Rejmánková et al. 1988, Pitcairn et al. 1994). Distribution of larvae in large wetlands (one to several square kilometers) has not been reported.

In our earlier surveys (Rejmánková et al. 1993), larval sampling was restricted to the margins of wetlands and to areas that were relatively accessible. Our next goal was to assess the larval distribution throughout a large wetland. We hypothesized that the majority of larvae will be found in the periphery of wetlands relatively close to sources of a blood meal (i.e., human habitation or pasture).

In addition to our interest in the spatial distribution of *A. albimanus* larval populations, we were also interested in the specifics of habitat selection by ovipositing females. Consistent absence of anopheline larval species in certain types of habitats and frequent presence in others have usually been attributed to selectivity exhibited by ovipositing fe-

males or to unfavorable factors in water that destroy eggs or larvae (Russel and Rao 1942). Orr and Resh (1992) demonstrated a clear preference of ovipositing Anopheles females, as well as larvae, for dense patches of an emergent macrophyte, Myriophyllum aquaticum Vell, which provides refuge from predation and enriched food source. We knew that algal mats were favorable habitats for A. albimanus larvae, whereas open water was not (Rejmánková et al. 1993 and unpublished data). We did not know whether adult females preferentially laid their eggs on the mats or whether they did not differentiate between algal mats and open water, but larvae only survived in the mats where they were sheltered against predators. Questions that we attempted to answer are as follows: What is the association of A. albimanus with cyanobacterial mats? Does larval density in wetlands change with increasing distance from the margins of the wetlands or houses/pastures? Do the ovipositing females discriminate between open water and cyanobacterial mats?

The results contribute to our understanding of habitat selection by *A. albimanus* females. Additionally, this research provides useful information of potential use for the control of malaria in Belize—a country experiencing recent increases in malaria rates (Polanco 1993).

Materials and Methods

Study Site Description. The diverse environment of Belize provides a variety of habitats for anopheline mosquitoes. Slightly over half of the country is characterized by hilly and mountainous areas and the rest is occupied by low-lying coastal plain (Wright et al. 1959, King et al. 1992). The overall climate of Belize is subtropical, with relatively constant temperatures throughout the year. The rainy season lasts from May/June through November. The Coastal Plain regions consist of lowlands with elevations of 0-20 m. Most of northern Belize, composed of the administrative districts of Corozal, Orange Walk, and Belize, is in the Northern Coastal Region (Fig. 1). The Northern Coastal Region is drained primarily by 2 river systems, the New River and the Rio Hondo. Surface and subsurface drainage patterns are quite complex. Coming from a soft limestone area, the water is saturated with calcium carbonate (lime) and often has a high calcium sulfate (gypsum) content. Limestone in the southern part of the region is covered by old strand deposits resulting in more acidic waters with a lower calcium content. Waterlogged areas support several types of swamp forest, both freshwater and mangrove, that are not favorable habitats for A. albimanus larvae. The herbaceous marshes dominated by tall emergent sawgrass, rushes [Eleocharis cellulosa Torrey, *E. interstincta* (Vahl) Roemer & Schultes and *E.* elegans (Kunth) Roemer & Schultes], and cattails with subdominants of both floating and sub-



Fig. 1. Sampling sites in Northern Belize (1-21). Arrows indicate Chan Chen (4) and Buena Vista (9) marshes where the transect sampling and oviposition experiment were conducted.

mersed aquatic macrophytes are more suitable anopheline habitats (Rejmánková et al. 1995). Of particular importance for *A. albimanus* production are marshes in limestone areas with sparse growths of rushes and sawgrass and abundant cyanobacterial mats. The mats usually consist of fine filaments of *Leptolyngbya* spp., which form most of the biomass and are intermingled with many different species of cyanobacteria. See Table 1 for a detailed list of species.

Table 1. List of species of cyanobacteria forming the cyanobacterial mats in the Buena Vista and Chan Chen marshes

Species	Buena Vista	Chan Chen
Leptolyngbya sp. div. (2 species)	D	D
Aphanocapsa intertexta Gardner	_	+
Aphanothece bacilloidea Gardner	+	_
A. opalescens Gardner	+	+
A. variabilis (Schill.) Komárek	+	—
Aphanothece sp.	_	+
Anacystis microsphaeria Gardner	+	+
Bacularia gracilis Komárek	+	_
Chamaesiphon subg. Chamaesiphonopsis sp.	_	+
Chroococcus aeruginosus Gardner	+	+
C. minutissimus Gardner	+	+
C. subsphaericus Gardner	+	+
Gloeocapsa cf. quaternata Kützing	-	+
Gloeothece ophalotecata Gardner	+	_
G. prototypa Gardner	+	+
Hassalia cf. discoidea Gardner	+	+
Johannesbaptista pellucida (Dick) Taylor &		
Drouet	+	_
Phormidium tortuosum (Gardner) Anagnostidis		
& Komárek	+	+
P. willei (Gardner) Anagnostidis & Komárek	+	+
Pseudanabaena cf. papillaterminata (Kisel.) Kurr.	+	+
Pseudanabaena sp.	+	_
Pseudanabaena sp. div.	_	+
Rhabdogloea sp.	_	+
Schmidleinema cubanum Komárek	_	+
Scytonema cf. tenue Gardner	_	+
Spirulina sp.	+	+
Synechococcus sp.	+	-
Tolypothrix cf. willei Gardner	+	-
Xenococcus sp.	—	+

D indicates the dominant species; +, species present; -, species absent.

Habitat Evaluation. The distribution of cyanobacterial mats in the Chan Chen and Buena Vista marshes was mapped with 1:3,000 scale color infrared aerial photography in February 1993. The resolution of the photography was 1–2 m and plant communities could be readily identified. Two categories of marsh were mapped: (1) marsh with cyanobacterial mats, represented by *E. cellulosa* or *E. cellulosa* mixed with sparse stands of *C. jamaicense*; and (2) marsh without cyanobacterial mats, represented by dense stands of *C. jamaicense*, *C. jamaicense* mixed with shrubs, or open water.

Transect Sampling. To assess larval distribution in the interiors of marshes, we selected 2 large marshes (Fig. 1) typical for their abundance of cyanobacterial mats. Both marshes are permanently flooded, 30–90 cm deep, with water level dropping $\approx 15-20$ cm in the dry season. Sampling was conducted once in the wet season (August 1993) and once in the dry season (March 1994). Each transect was 1,000 m long with sampling points located in 100-m intervals. At each sampling point, we collected larvae from 10 dips taken from the algal mats with a standard 350-ml mosquito dipper. Open water was not sampled because repeated previous experiences indicated no larvae in these areas. There are many fish present in these marshes and few if any larvae would survive in unprotected areas. In the wet season, 1st and 2nd stage larvae were counted together and so were 3rd and 4th stage larvae. In the dry season, each stage was recorded separately because more experienced team members conducted the sampling. Larvae were preserved in 80% alcohol and identified to species in the laboratory. The percentage of cover of both the cyanobacterial mats and emergent plant, *E. cellulosa*, was visually estimated in an area 5 by 5 m around each sampling point.

In addition to transect studies, we also sampled various sites in other marshes (Fig. 1) to determine the presence or absence of larvae of A. albimanus. These marshes were selected to represent a variety of natural marsh habitats in northern Belize for a study related to macrophyte distribution (Rejmánková et al. 1996) and mosquito sampling was not the primary activity. The marshes ranged in size from 1 to >100 ha, and they were all dominated by either monocultures or inixtures of C. jamaicense, Eleocharis spp., and T. domingensis. Twenty dips were taken in each marsh, presence of cyanobacterial mats and emergent vegetation was recorded and water samples were collected for water analysis. Distances from edges of these marshes to houses and pastures were measured from the land use map (King et al. 1992).

Oviposition Experiment. Frames 25 cm in diameter and 6 cm tall were cut from a PVC pipe. Nylon mesh was glued to the bottom of the frame and a strip of plastic bubble-wrap was placed around each frame as a float (Fig. 2). Two areas in the Chan Chen marsh were selected for placement of the oviposition frames, 1 with a dense cover of cyanobacterial mats and 1 with open water. Ten frames, loosely fastened by a string to a pole, were placed in each of these 2 areas. Of the 10 frames in each area, 5 contained cyanobacterial mats and 5 contained just water. Cyanobacterial mats placed in the oviposition frames were drawn from a ≈ 1 m² area of cyanobacterial mats that had been covered for 48 h by a window screen placed ≈20 cm above the mats to prevent mosquitoes from laying eggs on the mats. Because A. albimanus females need physical contact with an ovipositing surface, we were confident that no eggs were oviposited through the mesh. The frames were exposed for 48 h and then collected, each in its own plastic dish holding water, and transported to the laboratory. One, 2, and 3 d afterward, each frame was examined with a dissecting microscope to determine the presence of 1st stage larvae.

Climatological Measurements, Water, and CO_2 Analyses. Temperature, pH (combined pH, mV, and temperature meter, ORION 230) and dissolved oxygen (OMEGA Oxygen-meter) were measured at Chan Chen in both cyanobacterial mats and in open water at 4-h intervals for 24 h. Water samples representative of the whole water column were analyzed for calcium content using atomic absorption spectrophotometry. CO_2 emis-



Fig. 2. PVC frames used for the oviposition experiment. The frames, 1 with and 1 without cyanobacterial mats, were placed in a dense stand of mats, Chan Chen marsh, May 1994.

sions from algal mats were measured using the closed chamber technique (Mosier 1989). CO_2 was determined on Shimadzu 14A gas chromatograph. Fluxes were estimated as the change in gas concentration over time corrected for the ratio of chamber volume to surface area covered.

Results

Habitat Extent. Fig. 3 presents the maps of Chan Chen and Buena Vista marshes where the transects were located. The total area of Chan Chen marsh is 139.2 ha, of which 92.8 ha was identified as larval habitat (i.e., *E. cellulosa* or sparse *C. jamaicense* with cyanobacterial mats of various density). The area of Buena Vista marsh is 74.4 ha; 58.0 ha was identified as larval habitat. Chan Chen is characterized by a larger area of open water in the central, deepest part of the marsh. Most of Bnena Vista marsh is covered by sparse *E. cellulosa* mixed with cyanobacterial mats.

Larval Distribution Along Transects. The distributions of larvae along the transects are shown in Fig. 4. Numbers of larvae per dip in cyanobacterial mats did not significantly decrease with distance along either of the two 1,000-m transects. In



Fig. 3. Chan Chen (A) and Buena Vista (B) marshes based on 1:3,000 scale color infrared aerial photography taken in February 1993. Bold lines indicate the locations of transects.

the wet season, the average cover of cyanobacterial mats and *Eleocharis* was 7 and 10% of the water surface, respectively, for Chan Chen and 12 and 15%, respectively, for Buena Vista marsh. In the dry season, cyanobacterial mats and Eleocharis averaged 75 and 1% in Chan Chen and 35 and 15% in Buena Vista. The larval densities in cyanobacterial mats were Chan Chen 2.8 and 2.3 larvae per dip in the wet (August) and dry (March) seasons, respectively; Buena Vista 0.8 and 1.02 larvae per dip in the wet and dry seasons, respectively. These values are in the range of larval densities found for cyanobacterial mats in this region in previous studies (Rejmánková et al. 1993). The larval distribution, particularly at Chan Chen, did not seem to exhibit strong aggregation (at about half of the sampling stops along the transect the variance was equal or lower than the mean). In the dry season, we found a significant positive correlation between the number of larvae and the percentage of cover of cyanobacterial mat ($r^2 = 0.41$, P < 0.05, n =11) at Chan Chen; Buena Vista showed the same correlation but not statistically significant (r^2 = 0.34, P < 0.08, n = 11). In Buena Vista we found a significant negative correlation between number of larvae and density of emergent *Eleocharis* ($r^2 =$ 0.36, P < 0.05, n = 11).



Fig. 4. Mean \pm SD number of larvae per dip along a transect in Chan Chen marsh (\Box) and Buena Vista marsh (\blacksquare) in the wet season, August 1993 (A), and the dry season, March 1994 (B).

The larval age distribution was similar in both marshes in the dry season averaging 38, 36, 19, and 7% for 1st, 2nd, 3rd, and 4th instar, respectively.

Larval Presence/Absence in Marshes on the Northern Coastal Plain. Of the 21 marshes vis-

ited during the 1993 wet season and 1994 dry seasons, cyanobacterial mats were found in 11, and 9 of those were positive for A. albimanus larvae (Table 2). The test of independence between cyanobacterial mats and larvae showed a significant positive association (chi-square with continuity correction = 11.17; P < 0.001). In most marshes we noticed quite diverse populations of fish; poeciliids (Poecilia spp.) seemed to be the most abundant group. Cyanobacterial mats were usually very dense and seemed to successfully prevent fish and other predators from reaching mosquito larvae. Marshes without cyanobacterial mats were those that were dominated by cattails and those that were located in the southern part of the study area with lower concentration of calcium carbonate. The average distance from either houses or pastures did not differ between the group of marshes with larvae and the group without larvae (the average distance between houses and marshes 1.68 and 1.67 km; the average distance between pastures and marshes 1.92 and 1.63 km for sites with and without larvae, respectively). Water from marshes with cyanobacterial mats and larvae contained significantly higher concentration of calcium (t = 2.04, P < 0.05, d.f. = 19).

Oviposition. Results of the oviposition experiment are summarized in Table 3. There was no effect of the surrounding environment on the number of eggs oviposited as defined by number of first stage larvae that hatched. However, we found a significantly higher number of first stage larvae in frames with cyanobacterial mats (2-way analysis of variance [ANOVA], F = 15.55, df = 1, P < 0.001). Measurements of diel patterns of tem-

 Table 2. Distribution of cyanobacterial mats and A. albimanus larvae in herbaceous marshes in Northern Belize,

 August 1993 and May 1994

						Distanc	e from
	Location	Vegetation type	CB mats	Larvae	Ca ⁺²	Houses, km	Pastures, km
1.	Santa Cruz	Cladium/Eleocharis	+	+	158	1.5	1.3
2.	San Pablo 1.	Typha (loose)	+	+	80	0.3	0.5
З.	San Pablo II.	Typha	_	-	78	0.4	0.6
4.	Chan Chen	Eleocharis	+	+	175	1.0	0.5
5.	Storroch Creek	Cladium	+	_	77	4.0	4.0
6.	Laguna Cocos	Cladium	+	+	310	2.3	2.3
7.	San Victor	Typha		-	93	2.5	2.7
8.	Pulltrouser W.	Typha	-	-	113	0.5	0.5
9.	Pulltrouser S.	Typha	-	-	96	1.0	0.2
10.	Buena Vista	Eleocharis	+	+	41	1.5	4.0
11.	Honey Camp	Eleocharis	+	+	68	1.2	1.2
12.	By Progresso	Eleocharis	+	+	180	3.0	3.0
13.	Old N. Hwy, km 4	Eleocharis	+	+	28	3.5	3.5
14.	Old N. Hwy, km 10	Eleocharis/Cladium	+	_	36	0.8	0.8
15.	Old N. Hwy, km 12	Eleocharis/Cladium	+	+	38	1.0	1.0
16.	Northern Lagoon	Typha/Cladium	-	-	16	6.0	6.0
17.	Grace Bank	Eleocharis	-	-	7	1.3	1.3
18.	Sand Hill	Eleocharis	-	_	17	1.6	1.6
19.	Ladyville A.	Eleocharis		-	16	< 0.5	5
20.	Ladyville B.	Eleocharis	-	_	15	0.7	0.7
21.	Western Hwy.	Eleocharis	-	-	3	0.7	0.7

Cyanobacterial mats and larvae present (+), absent (-). Numbers 1–15 were located in the limestone area, numbers 16–21 were located in the sand deposits area. Concentration of calcium in marsh water is expressed in parts per million.

Table 3. Numbers	of 1st-instar A. albimanus t	hat
hatched in oviposition	frames following exposure in ar	eas
with and without mats	of cyanobacteria (ĈB)	

Environment	Environment inside frames			
outside – frames	CB mats	Water		
CB mats	3	0		
	1	0		
	3	0		
	5	0		
	0	0		
Mean ± SD	$2.4~\pm~1.9$	0.0 ± 0.0		
Vater	4	1		
	1	0		
	4	0		
	0	0		
	2	0		
Mean \pm SD	$2.2~\pm~1.8$	0.2 ± 0.4		

Treatments of oviposition frames were equally divided between frames with CB mats and frames with just clear water and subsequently exposed in marsh areas with CB mats and areas with open water.

perature and dissolved oxygen in water with and without cyanobacterial mats (Fig. 5) showed that during the early evening (expected oviposition time; Chadee et al. 1993) there is a higher temperature and lower oxygen content in cyanobacterial mats as compared to open water. Measurements documented in Fig. 5 are supported by similar results from other dates and other locations (E.R., unpublished data). After sunset, CB mats start emitting CO₂ as a result of intensive microbial and algal respiration. The CO₂ fluxes averaged 81 mg CO₂/m2/h from 1800 to 0600 hours.

Discussion

There are not many records available for A. albimanus larvae from natural marshes generally (Rodriguez et al. 1993) and only a few reports listing cyanobacterial mats as larval habitat for A. albimanus (Rejmánková et al. 1993). Cyanobacteria are sometimes regarded as detrimental or at least a deterrent to anopheline mosquito production (Russel and Rao 1942). According to many authors (as summarized by Faran 1980), A. albimanus larvae are often found in areas of secondary growth such as plantations and pastures. This is certainly true for most of the Pacific coast of Mexico, Guatemala, and El Salvador, where the natural vegetation has been substantially changed and replaced by intensive agriculture. Even from the Caribbean region, A. albimanus has been reported mostly from irrigated fields, semipermanent rain pools and from salt marshes (Taylor 1966). Yet the Caribbean coast, specifically on the Yucatan Peninsula, has large areas of relatively undisturbed natural marshes (King et al. 1992, Rejmánková et al. 1995, 1996). These large marshes support extensive areas of cyanobacterial mats and may provide larval habitats throughout the year. Similar marsh-



Fig. 5. Daily course of temperature (A) and oxygen concentrations (B) in open water (\bullet) and algal mats (\Box). Dotted lines indicate the expected time period of peak oviposition.

es can be expected in other limestone areas, e.g., Zapata Peninsula in Cuba and Caribbean coastal zones of Honduras and Venezuela.

Compared with results from other studies on *A. albimanus* larval habitats, our data on cyanobacterial mats show that some habitat-types dominated by graminoids (*Cynodon*, Cyperaceae, *Fimbristylis*), submersed macrophytes with periphyton, or both may have higher numbers of larvae per dip (Rejmánková et al. 1993, Rodriguez et al. 1993). However, with the exception of temporarily flooded pastures, no other habitat-types cover land areas as large as cyanobacterial mats on the Northern Coastal Plain of Belize. Since the larval sampling of 1993, 1994 reported in this study, we have repeatedly collected *A. albimanus* larvae from cyanobacterial mats in numerous other marshes on the Northern Coastal Plain (E.R., unpublished data).

Dipper samples do not provide estimates of absolute numbers of larvae per unit of water area. We opted to use a crude estimate of 1 dip as a sample for a surface area of 100 cm² (equals the size of the dipper), because in dense algal mats it would be difficult to sample a larger area. The inherent error of this estimate should be the same for all samples and is roughly equivalent to estimates used by other investigators. With this method, we estimated the average number of larvae per dip as 2.5 and 0.9 for Chan Chen and Buena Vista, respectively. Consequently, the average density of larvae can be estimated as close to 250 larvae per square meter of cyanobacterial mats in Chan Chen and 90 larvae per square meter at Buena Vista. Breeland et al. (1974) reported the larval densities of A. albimanus in the marginal zone of aquatic vegetation of Lake Apastepeque, El Salvador, to be

Location	Season	Habitat area, ha	CB cover, %	Larvae/ m ²	Larvae/ marsh × 10 ⁶
Chan Chen	Dry	92.8	75	230	160
	Wet	92.8	7	280	18
Buena Vista	Dry	58.0	35	102	21
	Wet	58.0	12	80	5.6

Table 4. Estimates of larval populations of *A. albimanus* in Chan Chen and Buena Vista marshes

Hahitat area estimated from the aerial photographs (see Fig. 2). The actual cover of cyanobacterial mats (CB) estimated on the ground during the transect sampling in August 1993 and March 1994.

high (≈220 larvae per square meter) in flooded grasses and low (≈ 1.2 larvae per square meter) in tules (Scirpus sp). According to their estimates, the anopheline larval population in the vegetated area of the lake would be close to 2 million. To estimate the total larval population of our 2 marshes (Table 4), we used the habitat areas of 92.8 and 58 ha for Chan Chen and Buena Vista, respectively (see Fig. 3). Even if these values are based on a 1-time estimate and may fluctuate somewhat, the total habitat area, according to our experience, does not change substantially. Note that on the aerial photographs, the larval habitat was identified as E. cellulosa or sparse C. jamaicense with cyanobacterial mats of various density. The density of cyanobacterial mats varies during the year; it is usually lower during the rainy season and higher in the dry season. The estimated numbers of larval populations per marsh $(5.6-160 \times 10^6)$ are quite high (Table 4). Because many marshes similar to these two exist throughout the Northern Coastal Plain, then even with high larval mortalities (often >90%, Service 1993) there are enough adults produced to justify calling this region a "Mosquito Coast."

Transect sampling did not show any decrease in larval densities with distance from houses or pastures. In the case of Chan Chen marsh, the village of Chan Chen is located ≈1 km from the beginning of the transect, meaning that the distant end of the transect was 2 km from houses. At Chan Chen, a pasture is located between the marsh and the village. In Buena Vista village, the nearest houses are ≈ 1.5 km from the beginning of the transect in the Buena Vista marsh. No apparent decrease in larval densities, with increasing distance from a village or pasture, may indicate that A. albimanus females travel long distances between blood meal sources (humans, cows, horses) and oviposition sites. Hobbs et al. (1974) and Lowe et al. (1975), in their studies on flight range of A. albimanus, reported that 500m and 1,000 m were the average flight distances in the dry season and wet season, respectively, and 3 km was the maximum flight distance. However, A. albimanus females may use other sources of blood, e.g., raccoons and birds from the surrounding woodland. Regardless, humans are important sources of blood for host-seeking *A. albimanus* females. Biting rates as high as 5.8 bites per minute were recorded in the village of Chan Chen (D.R., unpublished data).

The oviposition experiment confirmed that one of the reasons for the frequent presence of A. albimanus larvae in algal mats was the strong tendency of A. albimanus females to lay eggs in cyanobacterial mats. The question of why females choose cyanobacterial mats for oviposition deserves attention. What do habitats such as flooded pasture grasses, submersed macrophytes with periphyton, and cyanobacterial mats have in common that attracts the ovipositing females? According to Bentley and Day (1989), there are many similarities between mosquito host-seeking and ovipositing behavior. Mosquitoes make use of CO_2 odor plumes to locate hosts. After sunset, cyanobacterial mats emit somewhat higher concentrations of CO₂ because of the intensive respiration of the algal and bacterial communities present in these mats. Other habitats known to have high densities of larvae in Belize are submersed macrophytes with attached periphytic algae (Rejmánková et al. 1993). These communities can also be expected to release high fluxes of CO_2 after sunset. The potential of CO_2 as an ovipositional attractant requires further study. Higher temperatures in algal mats after sunset, compared with open water, is another potential signal for ovipositing females. In future studies we hope to define the basis for the attractiveness of cyanobacterial mats to A. albimanus mosquitoes.

Our study demonstrates that from the larval habitats available to A. albimanus in northern Belize, cyanobacterial mats are the most important habitats for the following reasons: mats are widespread and often permanent habitats, and they provide a rich food resource and refuge from larval predators. We have not conducted any experiments to prove larval habitat selection such as Orr and Resh (1992) did for other anopheline species. Simple observations showing that no larvae are found in dips taken from open water and that larvae seek refuge in algal mats when they co-occur in a dipper seem to be conclusive enough to suggest that larvae stay in cyanobacterial mats intentionally. We did show that the presence of cyanobacterial mats influences the selection of oviposition sites by A. albimanus females. A. albimanus is regarded as an opportunistic species (i.e., it would lay eggs in any suitable habitat that is available) as opposed to much more specialized mosquitoes [e.g., pitcherplant mosquito, (Wyeomuja smithii Coquillett)]. In such highly specialized species the habitat-selecting behavior can lead to an extreme genetic subdivision within a population (Istock and Weisbur 1987). It remains to be seen whether a long-term specialization of the northern Belizean population of A. albimanus for selecting cyanobacterial mats habitat has resulted in any ecotypic differentiation.

In conclusion, we have found that larvae of *A. albimanus* are closely associated with cyanobacter-

ial mats. These mats are common components of many marshes located in the limestone area of the Northern Coastal Plain of Belize. Larval density does not change with increasing distance from margins of the marsh or from human habitation or pastures. We interpret this finding as an indication that A. albimanus females make use of a wide array of vertebrate hosts and are not dependent on humans or domestic animals to maintain their natural abundance. Indeed, we found dense populations of A. albimanus adults in locations far from human habitation and domestic animals (E.R., D.R., unpublished data). Finally, A. albimanus females can discriminate precisely between open water and cyanobacterial mats when they are selecting oviposition sites.

The practical implication of these findings is that large and often permanent areas of productive larval habitats exist on the Northern Coastal Plain of Belize. So far, because of the relatively low human population density, most of the mosquitoes produced in these habitats are probably obtaining their blood-meal from other sources. But the increase in human population density may result in people moving closer to the marshes and, at the same time, destroying natural woodlands adjacent to these marshes. This would undoubtedly lead to a decrease in populations of wild vertebrates (the natural host) and an increase of human exposure to biting mosquitoes, accompanied by accelerated malaria transmission.

Acknowledgments

We thank Linda Reyes (Belize/U.S. Epidemiological Research Center) for her help with vehicle, supplies, and equipment support. We also thank J. Polanco (Vector Control, Ministry of Health) for his valuable advice. Thanks are due to the members of 1993 University Research Expedition Program for their patience and willingness to endure wading through mud for long miles each day. We thank Minghua Zhang and Noah Najarian (University of California) for technical support. Critical comments on the manuscript by Richard Andre (Uniformed Services University of the Health Sciences), Michael Pitcairn (California Department of Food and Agriculture), Marcel Rejmanek, (University of California), Mike Service (Liverpool School of Tropical Medicine), and 2 anonymous reviewers are greatly appreciated. Funding for this project was provided, in part, by the University of California Research Expedition Program (UREP), U.C. Davis Faculty Research Grant, and the Uniformed Services University of the Health Sciences through grant R087DB.

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Received for publication 7 June 1995; accepted 7 May 1996.

Rejmankova E., Roberts D.R., Manguin Sylvie, Pope K.O., Komarek J., Post R.A. (1996)

Anopheles albimanus (Diptera : Culicidae) and Cyanobacteria : an example of larval habitat selection

Environmental Entomology, 25 (5), 1058-1067

ISSN 0046-225X