Ecological Profile of *Culex* (Melanoconion) aikenii (Diptera: Culicidae), Vector of Endemic Venezuelan Encephalitis in Panama

PEDRO GALINDO and ABDIEL J. ADAMES

ABSTRACT

Preliminary notes are presented on the ecology of *Culex aikenii* (Aiken & Rowland), vector of Venezuelan encephalitis (VE) in the middle Chagres river basin of Panama. *C. aikenii* probably represents a complex of at least 2 closely related species with similar habits and both are involved in the natural transmission of VE virus. However, until taxonomic work now in progress is completed the name in its present broad sense will be used. Immature stages of the species are almost always found closely associated with the aquatic floating plant water-lettuce, *Pistia stratiotes*. Eggs are laid singly on the leaves. Larvae and pupae remain motionless for hours attached to air pockets under the *Pistia* leaves. When *Pistia* plants are dislodged from their anchorage by flooding, larva and pupae move down with them and may seed new areas where the plants become tangled and proliferate. These movements of *Pistia* seem to serve the double effect of restricting growth of local populations of *C. aikenii* and of serving as one method for dispersal of the species. Females have a broad spectrum of hosts both homeothermic and poikilothermic. They have a slight predilection for mammals over birds. Among the latter, herons are the preferred hosts. The species bites a variety of mammals, but seems to prefer rodents, except where there are large concentrations of domestic mammals, such as cattle. They feed on blood during dusk and dawn with peaks of activity occurring irregularly throughout the night. Females feed preferably on the ground, seldom going up to the canopy of trees in search of hosts. Man is usually bitten very low on the legs, so that people wearing shoes and long pants are seldom fed on.

*Culex* (Melanoconion) aikenii (Aiken & Rowland) appears to be the principal mosquito vector of endemic Venezuelan encephalitis (VE) in the Chagres river basin in Panama (Galindo and Grayson 1971). The importance of this species as a disease vector has led to the development of a study of its ecology in the middle Chagres river basin and the possible relationships between the population dynamics of *C. aikenii* and the incidence of VE in the area. Since some of the ecological information acquired is important to interpretations of other studies, a general ecological profile for the species is presented.

General Notes on the Systematics of *Culex aikenii*

Nomenclature of the Species

Belkin (1970) recently reviewed the nomenclatorial status of *Culex (M.) aikenii*. He re relegated the name *aikenii* to *nomen dubium* and resurrected 2 synonyms, ocososa Dyar & Knab and panocossa Dyar, to designate a southern and northern species, respectively, which in his opinion are being confused under the current usage of the name "*aikenii*." We think that the taxonomic status of the *aikenii* complex needs further clarification and pending completion of current studies have decided to continue the use of the name *aikenii* in its present broad sense. This decision was reached, after consultation with Dr. Belkin, as an expediency to disseminate urgently needed knowledge about a poorly known important vector or vectors of disease.

It must be pointed out that preliminary investigations indicate that both morphological forms, considered distinct species by Dr. Belkin, have extremely similar habits and both have been found to be involved in the natural transmission of VE.

Geographic Distribution

As will be discussed later, the immature stages of *C. aikenii* are intimately associated with the aquatic floating plant belonging to the family Araceae, *Pistia stratiotes* (water-lettuce) and the mosquito may be restricted to areas where the host plant is present. According to Stodola (1967) water-lettuce is tropicopolitan. In the Western Hemisphere it is known from Florida, Louisiana, Texas, along the Gulf Coast of U.S.A., and south to northern Argentina. However, the host plant seems to have a wider distribution than *C. aikenii* as this mosquito only has been reported (Stone et al 1959) from Mexico south to British Guiana. We have recently examined Melanoconion material from Belém, Brazil, received through the courtesy of Dr. T. H. G. Aitken, from which immature stages and adults of *C. aikenii* were identified. Dr. Pablo Barreto also donated to us a single male specimen from Tunaco, Columbia, near the border with Ecuador. These records extend further south along both coasts the known distribution of the complex.

Description of the Study Area

Physiography

The study area is located on both banks of the Rio Chagres between the Panamanian town of Santa Rosa and the Canal Zone town of Gamboa, including the lower course of the Rio Chilibre, a
tributary of the Chagres that runs into it below Santa Rosa (Fig. 1). Field headquarters for this study were located at Juan Mina, an old citrus grove downstream from the Rio Chilibre, where Gorgas Memorial Laboratory has maintained a field study station for many years. The study area is 8 km long and 1 km wide on each side of the river. The region is flat and swampy, at most places being no more than 25 m above sea level. The Rio Chagres is approximately 90 m wide and 8 m deep in the deepest part, at the level of Juan Mina. It is shallower and swifter above the mouth of the Rio Chilibre and broadens out toward Gamboa into a small lake. The numerous inlets and oxbows along the course of the river are choked with a variety of floating and emergent aquatic and semi-aquatic plants, the most common being: water hyacinths (Eichhornia azurea and E. crassipes), water lilies (Nymphaea spp.), water lettuce (Pistia stratiotes), water weeds (Hydrilla verticillata and Najas marina), water ferns (Salvinia auriculata and Azolla spp.), pickerelweed (Pontederia spp.), water grasses (Luziola subintegra and Paspalum repens) and water pier (Ludwigia natans). These masses of aquatic vegetation usually occur in mixed associations of several species with a dominant form, but occasionally may be found in pure stands or in mixed communities of many species without a noticeable dominance.

Madden Dam, located 4 km above the upper border of the study area, was constructed to control the flood waters of the Chagres and to store water in Madden Lake for use in the operations of the Panama Canal. For this reason, the flow of the Rio Chagres in the study area is largely controlled artificially by operations in Madden Dam. During the rainy season the river is subjected to periodic and sudden flushings when the dam gates are opened, which sometimes spill very large amounts of water within a short period of time. These flushings cause considerable change in the landscape of the study area. Floating plants which are loosely anchored along the oxbows and inlets, such as Pistia stratiotes and Eichhornia crassipes, are dislodged and washed downstream. In this manner, veritable islands of plant communities are moved toward Gamboa where this vegetation is trapped, gathered, and burned, to avoid clogging the main channel of the Panama Canal.

The Rio Chilibre, where most of our studies were conducted, is a sluggish meandering stream, which is about 27 m wide at its junction with the Chagres. Its lower course supports a variety of aquatic vegetation with a dominance of water-lettuce. Associations of this plant are found loosely anchored to the banks in extensive communities which at times of low water practically choke the stream. Floods of the Rio Chilibre may occur independently from those of the Rio Chagres, as downward flow along its channel is not directly influenced by operations at Madden Dam. Consequently, at times of heavy rains along the Chilibre watershed, its level may

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**Fig. 1.**—Map of the study area.
rise considerably while the Chagres remains low. On the other hand, when massive spillage takes place from Madden Dam and the Chagres rises rapidly, the flow of the Chilibre is reversed for at least one kilometer from its mouth, sometimes maintaining a backward flow for several hours. This effect causes a considerable rise in the water level with extensive flooding of the surrounding areas and corresponding movement of Pistia banks.

Along the left bank of the Chagres, just below Juan Mina, there is a range of hills known as Cerro Tigre dominated by 2 peaks which reach about 200 m above sea level. Along the right bank of the river, below Cerro Tigre, and facing a large lagoon, there is a 2nd flat ridge, known as Aguardiente, with a maximum elevation of about 100 m. Both ridges are covered with stands of tropical forest, transitional between the humid and deciduous types. Along the river banks the common trees noted were the thorny-barked "gallito" (Erythrina glauca) and several species of "higueron" (Ficus sp.), which are typical inhabitants of swampy 2nd growth forest.

Rainfall

We have no rainfall data for Juan Mina for the study period (September 1970 through September 1971). However, the Panama Canal Company maintains rain gauges at Madden Dam, above the study area, and at Gamboa, corresponding to the lower limits of the area under investigation. A 10-year average rainfall for each of these stations as well as the monthly totals for one year are presented in Table 1.

Temperature

Moll and Legler (1971) reported air temperature figures for Juan Mina gathered in 1965 and 1966. During January through April, temperatures were the highest during the day and the lowest during the night. The lowest and highest average maximum temperatures were recorded in November (28.1°C) and April (30.6°C) respectively. The lowest and highest average minimum temperatures were recorded in February (21.6°C) and June (24.2°C) respectively.

Material and Methods

Studies were carried out on both the immature stages and adults of the species. Larvae and pupae were searched for in all types of mosquito breeding sites, such as shaded and sunlit ground water, both running and still, with and without vegetation cover, in heliconias, treeholes, bromeliads, and water accumulation deep within animal burrows, etc. Adult collections were carried out by a variety of methods, such as light traps, animal-baited traps, hand collections from a variety of baits exposed around-the-clock, including man, horse, cow, pigs, rodents, and birds. Both male and female mosquitoes were collected from resting places by stirring them out of these places and capturing them with midge nets. Males were used for taxonomic investigations and females for population studies and to run precipitin tests on the stomach contents of specimens showing signs of having recently engorged on blood.

When it was determined that females of the species feed on blood only between dusk and dawn a program of all-night captures was instituted using one man on the ground and one 15 m up in the canopy of a tree; to avoid bias, collectors were shifted periodically. During September 1970, 11 such captures were carried out during consecutive nights. From October 1970 through September 1971, one all-night capture was made during the 1st week of every month.

Results and Discussion

The Immature Stages

The Habitat.—Larvae and pupae of C. aikenii are usually found associated with Pistia stratiotes. According to Stoddard (1967) this plant has rather exacting growth requirements which makes it difficult to grow in aquaria. It prefers well aerated, soft, slightly acid to neutral water (pH 6.5-7.0), and a highly nutritious substratum with plenty of organic matter. The plant reproduces either from stolons or seeds. Under ideal conditions young plants proliferate rapidly and in less than 45 days attain the floating stages, soon forming very large communities. On the Pacific side of Panama, along sloughs in the deltas of rivers which are rich in silt deposits, conditions are favorable for development of very extensive banks of Pistia which all but choke the sloughs for distances as long as one mile. In these communities P. stratiotes is almost always found associated with one or more species of small floating ferns (Salvinia auriculata and Azolla sp.). Plants of Pistia may be found mixed in associations with other large aquatic plants such as water-hyacinths, pickerelweed, water lilies, and water-grasses (Lutziola subintegra, Paspalum repens, and others).

Habits.—Larvae of C. aikenii have a special predilection for water-lettuce. However, critical sur-
vying to date has not been ample enough to allow definitive conclusions as to whether populations of this mosquito may be supported in the total absence of water-lettuce. In areas, like the Rio Chagres, where large *Pistia* communities are present and population densities of this mosquito reach very high levels, larvae have been collected from mixed associations of aquatic plants with a dominance of such species as *Pontederia* sp., *Eichhornia azurea*, *E. crassipes*, *Hydrilla verticillata*, and *Najas marina* but almost invariably in the presence of at least a few *Pistia* plants. On several occasions fairly heavy breeding of *C. aikenii* was detected in dense mats of an association dominated by *Ludwigia natans* mixed with a fairly abundant growth of *Hydrilla verticillata*, *Salvinia auriculata*, *Azolla* spp., and a few plants of the grass *Luziola subintegra*. This association forms a large matted surface of several meters in diameter where *aikenii* has been taken in numbers at least 200 m from the nearest water-lettuce plants. From this finding it becomes evident that more refined ecological studies are needed to determine the exact breeding requirements of this culicine mosquito. Despite present fragmentary knowledge of the factors limiting the breeding of *C. aikenii*, it may be safely stated that the species appears to reach high population densities only in the presence of communities of *Pistia stratiotes*.

Adames and Galindo (1972) have described the behavior of *C. aikenii* under insectary conditions and found that larvae will not develop normally in the absence of water-lettuce, but no other aquatic plants were tried. These authors utilized individual leaves of *Pistia* floating on the rearing medium and observed that all larvae congregate under the leaf and remain there motionless, unless disturbed, using trapped air pockets as a supply of oxygen. In the field, larvae also congregate under floating leaves maintaining an almost horizontal position which may afford them protection against natural enemies such as fish, naiads of mayflies, dragonflies and damselflies, dytiscid larvae, helcomatids, tanaid larvae, chaoborids, etc. (Dunn 1934).

Dispersal of Immature Stages.—Along the Rio Chilibre, which is subject to periodic floods during the rainy season, the banks of *Pistia* anchored along the meanders of the stream fluctuate in size continuously. During periods between floodings the banks proliferate rapidly from the edge toward the middle of the stream. As the flow of water increases during floods, the plants in the swiftest part of the current become dislodged from the rest of the bank and float downstream in patches varying in size from a single plant to clumps several meters in diameter. The larvae and pupae of *C. aikenii* remain attached to the leaves of the plants and move downstream with them. As the floating clumps of *Pistia* become tangled along the Rio Chagres inlets they give rise to fresh communities which proliferate very rapidly. The larvae which have been carried down with the plants may give rise to small population foci in these localities which expand with the growth of the *Pistia* communities. When large spillage occurs from Madden Dam, the flushing effect along the Rio Chagres washes down the *Pistia* banks and the population of *C. aikenii* along the main river channel drops rapidly. Thus, movements of *Pistia* along the Rio Chilibre and Rio Chagres act as a restraining mechanism of local populations of *C. aikenii* and as a method of dispersal for the species. Pupae also have the habit of clinging to air-bubbles under the *Pistia* leaves, remaining in position unless violently disturbed, and moving downstream with dislodged plants.

**Adults**

Emergence from Pupae.—Adults usually emerge from the pupal case at night. This appears to be a protective mechanism against certain deleterious factors to which adults would be subjected if they came out during daylight hours. The first of these factors is direct sunlight. Since the host plant almost always occurs exposed to the direct rays of the sun, imagines coming out of the pupal case during the day would be subjected to heat injury or death. The second is the presence of an abundance of diurnal predators which are active on the *Pistia* banks, particularly dragonflies and spiders.

Mating.—Coupling of the sexes has not been observed in the field. Adames and Galindo (1972) did not describe the actual act of copulation under colony conditions, but state that mating probably takes place during the short crepuscular periods at dusk and at dawn and begins from 2–3 days after emergence from the pupal stage.

Feeding Habits.—Females start to take blood at about the same time that sexual activity commences and may feed before or after mating. Large numbers of females have been taken in traps baited with golden hamsters (*Mesoceicetus auritus*), cotton rats (*Sigmodon hispidus*), spiny rats (*Proechimys semi-inus*), and chickens. Large numbers also have been collected by hand collecting from man, horse, pig, golden hamster, and common opossum (*Didelphis marsupialis*). C. H. Tempelis and P. Galindo (unpublished) are conducting a long-term study to determine the blood meal of wild-caught freshly engorged *Melanocorion* females by the precipitin test. While data are still being processed, it may be stated that *C. aikenii* has a wide range of hosts, which includes both homothermic and poikilothermic animals, but with a decided preference for the former. There is a slight predilection for mammals over birds. Among the latter, herons seem to be the preferred hosts. There appears to be a wide variety of selection among mammals, which includes primates, bovines, equines, edentates, chiropterans, carnivores, marsupials, and rodents. Rodents seem to be selected most often when there is no dense concentration of large domestic mammals in the area under study. However, when the sample is biased by the presence of numerous large domestic vertebrates, such as cattle, in the immediate vicinity of the collecting site, antisera for these mammals
yield the highest number of positives in the precipitin test.

Females usually fly very close to the ground and thus prefer to feed on the lower extremities of the hosts. On man, females almost always feed below the knees and preferably on the feet, so that people wearing shoes and long pants are seldom bitten. Rodents and marsupials are bitten on the feet and on the ear and nose. Pigs, lying down, are attacked around the legs and on the genital organs. Horses and cows are almost always bitten on the legs, close to the hoof. No observations have been made to determine the area on the body where birds are bitten.

Vertical Distribution.—Fig. 2 shows the number of *C. aikenii* per 10 man-hours collected on the ground and in the canopy during each of the hours from dusk till dawn. These collections were made on consecutive days from September 8, 1970, through September 18, 1970, and on the 1st week of every month from October 1970 through September 1971.

From the data in Fig. 2 it is apparent that *C. aikenii* females in the study area have a decided preference to feed on the ground and seldom fly to the branches of trees in search of hosts.

Daily Activity Cycle.—In investigations conducted previously by S. Sribhongse and P. Galindo (unpublished data) in the study area, no *C. aikenii* females were taken attacking man during the daylight hours, even in deep forest during dark days. Data included in Fig. 2 indicate that the species will feed throughout the night and that peaks of attack occur irregularly between dusk and dawn. Environmental factors involved in the production of these peaks have not been determined.

Annual Cycle of Abundance.—From data acquired to date, no conclusions can be reached as to annual fluctuations in the *C. aikenii* populations of the Rio Chilibre. Monthly figures presented in Fig. 3 are not statistically comparable because these collections were made only once a month during the 1st week of every month under variable meteorological conditions. Examination of data in this graph seem to point to a sharp population drop from February to May which corresponds to the drier months of the year (Table 1). However, it must be pointed out that during these months Canal Zone authorities regularly sprayed the Rio Chilibre with solutions of 2,4-D, a herbicide which is deleterious to *Pistia* plants, thus greatly reducing in size communities of this plant along the river. This in turn reduced the breeding areas of *C. aikenii*.

Oviposition.—Adames and Galindo (1972) illustrated masses of eggs of *C. aikenii* laid singly on a *Pistia* leaf in a laboratory colony. In the field, eggs are also laid singly on *Pistia* leaves attached close to the surface of the water. However, even in prolific breeding places only a few eggs have been found on a single leaf, so that we have failed to notice in nature the accumulation of eggs on a leaf which occurs in laboratory colonies.

Diurnal Resting Places.—In laboratory colonies, both males and females tend to seek *Pistia* plants as diurnal resting places. In the field, no adults have been found in banks of plants fully exposed to the sun. However, many males and females congregate on water-lettuce plants in the periphery of the banks in the shade. They also seek tall grasses and sedges along the edge of the breeding areas and may also be found resting in deep moist crevices in the ground. At night, gravid females come out of these
resting places and disseminate over the *Pistia* banks to lay their eggs. On one occasion 2 gravid females were collected early in the morning in a clump of *Pistia* that had dislodged from the Rio Chilibre and was moving into the Rio Chagres. Thus, it is possible that movements of *Pistia* during the night may regularly transport gravid females. This may constitute a method not only for dispersal of the species but also for dissemination of VE virus by gravid females that have previously become infected by feeding on a viremic vertebrate host.

REFERENCES CITED


