ARTICLES

BEHAVIOR PRECEDING MIGRATION IN THE SALT-MARSH MOSQUITO, *AEDES TAENIORHYNCHUS* (WIEDEMANN)

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The mechanics of the early stages of insect migration have been studied in but very few species. Two outstanding examples are the desert locust (*Schistocerca gregaria* Forskål) as summarized by Kennedy (1951) and the southern white butterfly (*Ascia monuste* Linnaeus) as described by Nielsen and Nielsen (1950). In these two migratory insects the behavior leading to the migratory exodus has been both described and related to the migration itself. Because of their large size the diurnal migrations were more easily observed. Corresponding studies of the migratory but small and nocturnal salt-marsh mosquito, *Aedes taeniorhynchus* (Wiedemann) have been under way in Florida since 1951, by the group at the Entomological Research Center of which I am a member. Previous to that year nothing advancing our knowledge of the mechanics of mosquito migration had appeared except the pioneering and monumental contribution of Smith (1904). The present paper is the second report on the premigration behavior, being a sequel to the paper by Nielsen (1958). Background information on the life history, behavior, and migrations of this mosquito may be culled from earlier works by staff members of the Entomological Research Center (Nielsen and Nielsen, 1953; Nielsen and Haeger, 1954, 1960; Provost, 1952, 1957; and Haeger, 1955, 1958).

Nielsen (1958) reported that new adults of both sexes leave the emergence site when 6 to 13 hours of age, provided it is in the dark period of the 24 hours, but we have found the minimum age at twilight exodus to be most often 6 to 8 hours. If large numbers were of that age or older a spontaneous mass departure would then take place at dusk. Nielsen assumed these departures initiated the migratory flight. The degree of hypopygial rotation was used as a measure of age in departing males. The departing females sampled had immature ovaries and empty spermathecae, proving they had not yet mated. Subsequent to these observations it was learned that mating did at times occur before the migratory exodus (Haeger, 1955; Nielsen and Haeger, 1960) as did also nectar feeding (Haeger, 1955). The present paper describes in detail the behavior observed preceding migratory exodi of this species in Florida, including some of the largest mass flights of mosquitoes ever reported.

Since one of the primary objectives of this paper is to report on sexual behavior prior to migration, it is important to know that males commonly attain hypopygial rotation of over 135° in from 12 to 18 hours and some as early as 10 hours (Nielsen, 1958). It is also well to remember that pupation reaches a daily peak at sunset while the pupal duration is a function of temperature alone (Nielsen and Haeger, 1954). Another pertinent fact is that mating normally occurs before the females start biting or the males swarming, both latter habits being usually exhibited by a brood of adults when three days or so of age (Nielsen and Haeger, 1953). And, finally, it is recalled that the migration of this mosquito may readily disperse a brood 25 or more miles (Provost, 1952, 1957).

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BROOD I. FORT PIERCE

On September 12, 1952 in the course of a dispersal experiment with radioactive-marked mosquitoes, thousands of copulations were seen among the departing migrants at twilight. This was our first observation of mass mating during an exodus, giving us the first intimation of where and when the truly significant mating occurred for a brood of *A. taeniorhynchus.* The details of this observation are given by Nielsen and Haeger (1960, in press). We were now alerted to the fact that mating under natural conditions could be better understood after closer scrutiny of initial departures from the emergence sites.

BROOD II. SANIBEL ISLAND

The second case of mass mating behavior was observed in the marsh under totally natural conditions. It occurred on the evening of May 21, 1953. The emergence site for this brood was on the north shore of Sanibel Island, facing San Carlos Bay and 1-3/4 miles west of the ferry landing. It consisted of a 2–3 acre black mangrove (*Avicennia nitida*) swamp known as the "Dead Forest." Many of the mangrove trees had died several years before, but young trees (4–10 feet tall) were now replacing the old, most of which had rotted and fallen to the ground. Patches of pickleweed (*Batis maritima*) were well established throughout the sunlit spaces on the marsh floor. These *Batis* areas made excellent egg-laying sites for the adult female mosquitoes. Living trees completely surrounded the dead area, even along the beach road but only an occasional old tree survived in the stricken area.

The previous brood was produced in April by high tides and resulted in a large emergence at the Dead Forest area. A seeming diversion here is necessary to clarify existing conditions of this previous population and its behavior up to the emergence of the May brood. It was during evening swarming studies in April that the first nectar feeding adults were observed by Dr. M. W. Provost and the author. This was a very important discovery as will be seen later when the potential of this habit was realized. During the first week after an emergence, nectar feeding commonly occurs each day and is easily observed. After about 10 days there is usually a sharp decline in feeding, on the 12th day only rarely seen, and after 13 days practically no nectar feeding occurs even though nectar may be plentiful in the flowers of as many as six major honey plants, in leaf-nectaries of another, and aphid honeydew is available. Returning now to May 21, the day of the big emergence in the Dead Forest, we find this was 27 days after the April brood emerged; nectar feeding no longer occurred, male swarming was over, and very few adult females were seen in either biting or light trap catches. Many thousands of eggs had been laid in the *Batis* and under logs and leaves at the Dead Forest during the 2–3 weeks previous to the May 16 tide flooding. The present brood of larvae was estimated to consist of several million animals. The development of the larvae was carefully watched and by the afternoon of May 20 about 50 percent had pupated but none had emerged. The next morning, May 21, at $08^h30'$ an inspection of the breeding area revealed that a great number of males had emerged sometime during the night. The emergence continued through the morning and early afternoon to $15^h00'$ when only a few stragglers were still emerging. The greatest concentration of emergence was among *Batis* plants and pneumatophores (aerial roots) of the black mangrove, *Avicennia,* where most of the pupae had congregated into large raft-like masses. The young trees, *Batis* plants, and aerial roots were literally covered with resting adults (see Figs. 1, 2). All the *Avicennia* trees were in their full splendor with terminally clustered white blossoms. Hundreds upon hundreds of the new mosquitoes were feeding on the blossoms but only to the 3–4 foot adult resting levels. They would walk about on the foliage and flowers while searching for the exceptionally fragrant nectar. Two hundred and fifty adults were counted on the ven-

FIG. 1.—Adult *Aedes taeniorhynchus* emerging from a large raft of pupae. Black mangrove aerial roots in center of picture are covered by adults 1–2 hours of age. *Batis* stems and leaves can be seen on left half of picture.

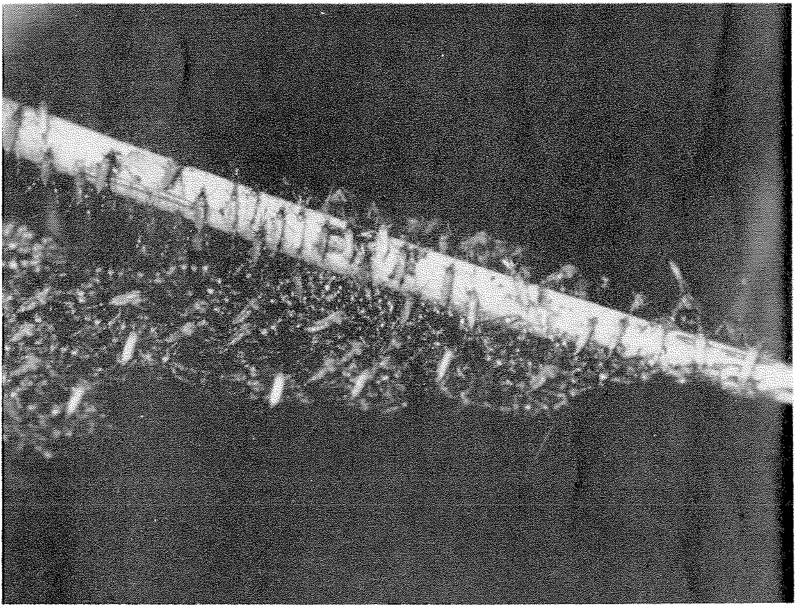

FIG. 2.—A close-up view of *Aedes taeniorhynchus* emerging from a corner of a raft of pupae.

tral sides of 5 mangrove leaves (because this side was favored over the top surface); the sex ratio was 3 ♂ to 1 ♀; compared to a nectar feeding ratio of 2 ♂ to 1 ♀ out of 150 adults counted on flowers. (These last observations were made between $15^h00'$ and $16^h00'$.) At $16^h00'$ I left the area to prepare for the evenings observations. Sunset was to be at $19^h06'$.

a. First Exodus of Brood II. Upon returning it was found that the adults were rapidly ascending into the higher tree canopy. Flower feeding continued to increase among both sexes. At this time they were gracefully flying to the flowers instead of walking over every flower head. By $19^h10'$ the feeding took place up to a height of 18–24 feet. There was such a great number feeding that they actually pushed one another aside to obtain nectar from the small flowers, the corollas of which measure 5 mm at the widest point. At this time ($19^h10'$) the sex ratio of nectar feeders was 2 ♂ to 5 ♀ (10:25). At $19^h15'$ great numbers were moving up to the very tops of the tallest trees, 24–30 feet high, nectar feeding was continued by many individuals up to the take-off time. A few mosquitoes were now ($19^h17'$) leaving on the initial migration. The weather was calm and a beautiful sunset was present, brightest in the north-west quarter. At $19^h20'$, 14 minutes past sunset, large waves of adults started leaving the branches in front of me as well as higher up, all seemed to be flying toward the brightest part of the sunset—the mass migration was on. A similar exodus into the sunset had been observed on April 22; also under conditions of complete calm. Five minutes later, $19^h25'$, they left in larger waves as if by signals, probably according to age groups, depending on time of emergence (see Fig. 3). No mating was seen yet, and I was wondering if it would take place. The primary observation site was about 4 feet east of a bushy black mangrove. The observer faced west towards a lateral branch 8 feet above the marsh floor, where a patch of sunset lighted sky shone through the foliage. At $19^h30'$ (24 minutes past sunset) nectar-feeding was still going on right up to the time of exodus. Many specimens could be seen with clear abdomens full of nectar; males did not hold nearly the quantity that females could. Still larger waves were leaving at $19^h31'$. The first matings now occurred at $19^h32'$ (26 minutes past sunset). Air temperature was 27.5° C.; still calm with not a leaf stirring. Such great numbers were now leaving that distinct waves were less noticeable. Fifteen copulations (in 2 minutes) were seen to occur immediately after the mosquitoes flew off the branch and its flower heads. The peak copulation period was during the next seven minutes, $19^h38'$ to $19^h45'$ (32–39 minutes past sunset) when it was estimated that 75 percent of all females leaving this branch were caught by males by the time they had flown 3–12 inches upward. After copulation these participating specimens continued to fly up at an angle toward the light western sky until they were lost from sight above the forest canopy. During this 7-minute period 98 complete copulations were counted. Several times two or three males would try to mate with the same female. In such cases the ball of fighting mosquitoes was very spectacular, usually one male succeeding in copulation. It was now $19^h50'$ and the number of departing migrants was tapering off (44 minutes after sunset) with some mating still taking place practically to the end of the departure. This exodus lasted 33 minutes and matings were observed over an 18-minute period. One hour later, at $20^h50'$ there was still a great singing of mosquitoes (high-pitched) in the air among or above the tree canopy which sounded like a "milling-about" flight. If they were migrants they did not seem to be going anyplace. No male top swarms were seen. The number of both sexes feeding on flower nectar was greatly reduced; these animals apparently were too young to leave.

Since only an occasional nectar-filled adult had been collected in the light trap two miles east at Punta Ybel during the past two weeks it was decided to check the light trap collection carefully on this exodus night of May 21, 1953, for this

Fig. 3.—An exodus of *Aedes taeniorhynchus* in the Hob Horse Cove area. As the adults fly from the low *Batis* vegetation below picture angle, most individuals fly into the wind which is blowing from right to left. The dead branches (upper center) and twigs (at right) are *Avicennia nitida.*

point. Between 21^{h}30′ the light trap caught about 100 ♀ *A. taeniorhynchus* and 1 ♀ *Aedes sollicitans* (Walker) containing nectar, but not a single male was collected either with or without nectar. The next run from 22^{h}30′ to 23^{h}00′ caught about 50 ♀ *A. taeniorhynchus* and 4 ♀ *A. sollicitans* and still no males. These females all seemed to be recently emerged as shown by their perfect and beautifully scaled appearance. On the night of May 22 there were a great many males in the light trap, a good number of these also contained nectar. Each night's collection from May 23 to May 31 was examined and found to contain many nectar-fed animals of both sexes. There was no known emergence closer than two miles west of this trap, that being the Dead Forest area. The fact that no males were collected on May 21 by 23^{h}00′ but many on May 22 may be accounted for by three possibilities; (1) the main migration was west or northwest, (2) the males dropped out short of the lighthouse on Punta Ybel and continued on to that point the second night, (3) or the second night's migration went more towards the east (Provost, 1952, 1957, found in both of his experiments that males were seldom attracted to light traps beyond two miles from the emergence site). The interior sloughs on Sanibel Island were not breeding during May, 1953.

b. Second Exodus of Brood II. On the second day of emergence (May 22) at the Dead Forest, there appeared to be about the same number of adults emerged by 15^{h}00′ as the day before at this hour, but the sex ratio of males to females was 1:1 instead of 2 or 3:1 as observed the previous day. The same behavior of resting and feeding was observed. At $17^h45'$ E. T. Nielsen and I watched the start of their ascent into the trees, this phenomenon occurred 45 minutes earlier than on the previous day due to clouds practically obliterating the sunset. Eight complete copulations were seen during the six-minute period between 24 and 30 minutes after sunset. It was now $19^h36'$ and rain and poor light made further observations at the site (under the trees) impossible. There was loud humming above the tree tops so a nearby tree was climbed to facilitate observations since there were still a few light patches of sky above and east of the dark clouds. Between these two sites the tree canopy was open for about 20 feet. From my vantage point, standing on a limb 15 feet above the marsh, I could observe the great mosquito activity near the tree tops. Since my height is 6′4″ the view at eye level was about 21 feet above the ground. I was practically among the singing, flying horde of mosquitoes. Above the tops of nearby dead trees very large top swarms were seen undulating back and forth like a cloud during the ascent of those which were leaving by the tens of thousands, supposedly on the migration. The closest swarms were 15 feet to the southwest and above my view at about a 30° angle (Dr. Nielsen was on the ground below as I gave him an account of the happenings at these levels). Copulations might have been taking place but the light intensity was too low to tell this. The interesting point was that swarms were formed on this second night when the oldest males were not much over 42 hours of age. This number of hours is given under the assumption that some of the adults observed the previous day at $08^h30'$ were emerging during the night of May 20–21 (arbitrarily set at $24^h00'$ on May 20). Later (October 16, 1958) it was found that evening swarms formed when the males were 22 hours of age.

Brood III. Hob Horse Cove

The third and largest brood ever observed during the initial stages of migration was in August 1955 and involved some 60,000,000 specimens, according to estimates made of pupal raft density and extent. This large brood was located in an *Avicennia-Batis* salt-marsh association on the river side of the offshore island beach-strand on the east coast of Florida and about 1/4 mile north of the line separating St. Lucie and Indian River Counties. "Hob Horse Cove" area is ecologically similar to the Dead Forest at Sanibel. The exodus study area lies along the west side of the oak-palmetto zone which gradually slopes upward to the sand dunes which extend 1/4 mile beyond to the Atlantic Ocean.

A natural seepage area occurs at the juncture of the upland oak-palmetto zone and the transition zone. Here are found the usual *Conocarpus erectus* (buttonwood), *Laguncularia racemosa* (white mangrove) and *Batis maritima* (pickleweed). Spring and wind tides flood the marsh up to this juncture. Extending westward there is a narrow sandy salt flat about eight feet in width, on either side of which *Batis* grows luxuriantly to a height of two feet or more. The sand flat and the *Batis* together form an open treeless area 18 feet wide by 100 feet long. To the south the open area abruptly joins some very large black mangroves and on the north it merges into a red mangrove (*Rhizophora mangle*) thicket. Between the black mangroves (to the south of the sand flat) the soil is soft silty peat and supports a thick growth of *Batis* in the sunny spots. It was in this vicinity that part of the large emergence took place and the following descriptions of exodi were observed. West of the sand flat for 150 to 200 feet there is a dense black mangrove forest, 35 to 40 feet high; the long axis running in a general north-south direction. The irregular forest floor in the most densely shaded or pot-hole areas contains only leaf litter, dead branches and numerous pneumatophores, but in sparsely shaded or dead tree areas *Batis* has invaded from the margins of this zone. Immediately west of this forest lies a wide (1/4 mile) expanse of *Batis* marsh, dotted here and there with orchard shaped, squatty trees no more than 15 to 18 feet high. All of these marsh plant communities held a high *A. taeniorhynchus* egg index (which had been deposited over a period of more than six weeks). It was from this entire marsh area that the brood described below resulted.

On Sunday, August 7, 1955, Hurricane "Connie" passed east of Vero Beach, 500 miles out to sea. The huge ground swells caused by the storm resulted in high tides which flowed into the inlets at Ft. Pierce, Stuart and Sebastian, causing the interior lagoon, viz., the Indian River, to overflow its banks. By August 9 and 10 the whole marsh was covered with 10 to 18 inches of water which hatched most of the viable eggs on the marsh. All flooded marsh areas on both sides of the river were teeming with large larvae on August 13. Pupation started in the Hob Horse Cove area on August 14 between $14^h30'$ and $16^h00'$.

The first day of emergence was well on its way at $10^h00'$ on August 16, with peak emergence about $11^h30'$. A collection of 500 of these adults revealed that the sex ratio of this emergence was 15 ♂ to 1 ♀. At $16^h30'$ the water temperature was 30° C. and the air temperature 28.5° C. At $16^h45'$ the older individuals were observed climbing, by short flights, into trees up to about 8 feet above the *Batis* and pneumatophore resting sites near the ground, and by $17^h15'$ many had reached the 15-foot elevation among the tree branches. There were almost no flowers at the emergence resting sites, only a few flowers of *Conocarpus* being present while the *Avicennia* blossoming season was past, so that nectar feeding prior to the exodus could not be observed for this brood.

a. FIRST EXODUS OF BROOD III. Sunset was at $18^h59'$ and the exodus started 16 minutes later at $19^h15'$. The initial waves of adults leaving the branches were very small, but soon a loud hum filled the air as larger waves became airborne. At $19^h20'$ when a dark cloud came over and obliterated the sky overhead (leaving only a thin area of sunset in the west), they started leaving *en masse* by $19^h30'$, probably because the light was lowered so rapidly (see Fig. 3). By $19^h35'$ no mating had been seen and no swarms of males formed. A dead calm prevailed and there was a hush over the land; the high pitched singing above the trees which was heard at Sanibel after the first night of exodus was missing here. From $19^h30'$ to $19^h45'$ adults feeding on the few *Conocarpus* flowers were studied and counted, there were 46 ♂♂ and 2 ♀♀. There were some adults biting at the edge of the hammock but out in the marsh proper there were very few biting. Apparently the biting mosquitoes were not from this area.

August 17 was the second day of this large emergence. I arrived at $10^h00'$ and already there were several million adult mosquitoes resting on the vegetation to an elevation of about 3 feet; in many cases both sides of the leaves of *Avicennia* seedlings were occupied, the undersides being completely covered with mosquitoes. There were three species of warblers engorging on the young adults resting on red mangrove trunks and roots, and in an open spot a sandpiper was making a meal of those resting on fallen leaves. The numerous rafts of pupae and larvae ranged in size from 10 × 12 feet to 20 × 40 feet (a raft of pupae consists of dense aggregation of 4th stage larvae and pupae which remain together and emerge at focal points among emergent vegetation, roots or leaves). Small fish were numerous and very voraciously feeding along the outside edges of these rafts. Whenever a minnow found itself enclosed by a portion of the raft of bobbing pupae and larvae it would immediately become unusually nervous and dash for open water. This rafting or balling-up seemed to serve as a protective device against aquatic predators.

Between $10^h30'$ and $11^h25'$ the greatest peak occurred. The surfaces of the rafts were now literally blanketed with newly emerged adults resting (while their wings dried) on the pupal skins and even on the backs of other pupae which were ready to emerge themselves as shown by their inactivity at the water's surface (see Fig. 1). All of the rafts in the vicinity had been measured by $12^h55'$ and the percent emergence of each recorded; many rafts were 100 percent emerged at this hour.

b. Second Exodus of Brood III. Mr. E. J. Beidler (Director, Indian River Mosquito Control District) assisted me in this set of observations. At $19^h00'$ many of the mosquitoes had ascended to a height of 6 feet into both black and red mangrove trees and ten minutes later they had reached 15–20 feet into the branches and tops of some trees. All at once at $19^h12'$ (14 minutes after sunset) the exodus started, with adults flying off branches and ground vegetation, going almost straight up until they were flying close to, but above the tree canopy. A few matings were seen when only small waves of mosquitoes were rising from the *Batis* plants and passing in front of the observers standing on the ground. Suddenly at $19^h13'$ (one minute after the exodus started) a massive movement of ascending mosquitoes began to almost darken the sky. This flight activity was observed for four minutes. The participants were scrutinized for further copulations, but no more were seen after the first minute of exodus. At this time, $19^h17'$, the author climbed a large black mangrove tree for closer observation of the flight above the trees. It was soon seen that the flight immediately above the observer's head consisted of a great band of millions of mosquitoes, all moving in unison on a southward upwind course (wind so low, almost imperceptible) in a compact undulating mass-flight. This band appeared to be 2–4 feet in thickness, vertical aspect, whereas the east-west width could not be ascertained (probably several hundred feet wide corresponding to the width of the principal north-south emergence area). Figure 4 shows the relative position and unidirectional southward upwind flight in relation to the vegetation of the marsh. It could best be compared to a huge belt or tread of a caterpillar tractor moving on rollers over the tops of the trees, only missing them by a few inches and dipping down between. At this time the air temperature had dropped about 2° C. below the $16^h00'$ reading of 31° C., a bright band of sunset sky remained to observe against, and a trace of air continued to come from the south (as tested by a wet finger). This migration had its maximum boost at $19^h20'$ or 8 minutes after the migration started. A sample of the migrating stream of mosquitoes was taken by sweep net at $19^h23'$ from above the tree in which the author was standing. Later, about 50 of these were examined; all were *A. taeniorhynchus;* and the ratio of males and females was almost exactly 50:50. At $19^h25'$ the exodus was over, the migrants had com-

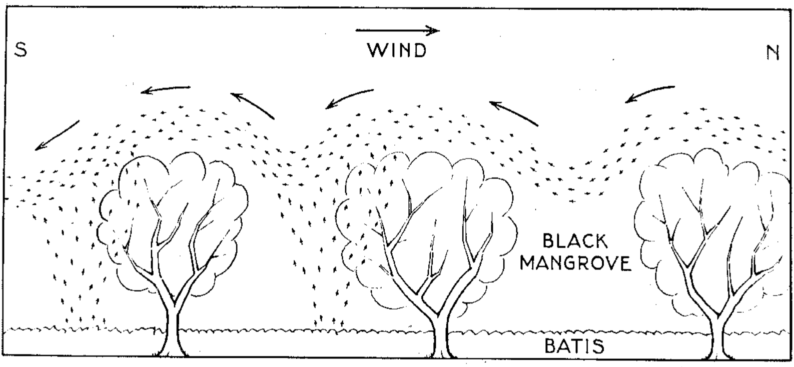

Fig. 4.—A schematic representation of the *Aedes taeniorhynchus* ascent and exodus and actual start of migration above the black mangrove trees.

pletely disappeared, and all was quiet in place of the high pitched, frenzied humming of millions of wingbeats. It was as if the observers had walked into a soundproof room. It was difficult to realize that we had actually seen a portion of the migration and that it took a definite direction of flight. Apparently no swarms formed and no high pitched singing could be heard after the migration was over, comparable to that observed at Sanibel Island on the first night at the Dead Forest study area. The *Batis* ground cover still contained a few thousand mosquitoes not yet old enough to leave.

The observation of this well-defined directional migration was possible because the location of the observation post was several hundred yards upwind of a large percentage of the breeding area. If the departing individuals had all left from the observation point, as in the other cases, this would never have been seen. The vast majority of males were too young for mating to take place.

c. THIRD EXODUS OF BROOD III. On this third day of emergence it was estimated that about 10 million adults had emerged by $13^h00'$. This day's emergence was not observed systematically as the two previous days were, but it is assumed that it followed about the same pattern. On this day Messrs. Beidler and Oscar Fultz came along to observe the exodus. On the way to the marsh large black clouds were noticed south of the emergence area. Presuming that this clouded condition (by lowering the light intensity) might hasten the ascent and the departure I drove to the observation point as quickly as possible. At $18^h50'$ as the party walked through a glade of *Bidens* and *Eupatorium* at the trailside (75 feet east of marsh) hundreds of *A. taeniorhynchus* of both sexes (from emergences of two previous days) were feeding on nectar in the flower heads of 6–7 feet tall *Eupatorium* plants. After watching the nectar feeding for three or four minutes we went on to the breeding area 150 feet to the west. It was now $18^h55'$ and the large black cloud to the south and west was obscuring the sunset. At this hour many of the mosquitoes were already in the black mangrove trees and a few had begun to leave. The first departure occurred 17 minutes earlier than the evening before when no clouds were present. This was undoubtedly due to the reduced illumination. Five minutes later at $19^h00'$ (2 minutes after sunset) they were leaving *en masse*.

Two observers stayed on the ground while the author climbed the same black mangrove tree from which he observed the directional flight the evening before. Those adults which left from resting sites in the tops of 2 feet high *Batis* plants left directly from there without first climbing the trees for the take-off. The same phenomenon had also occurred on the previous two evenings, but not quite to the same extent. As during the previous two twilight exodi the ascending adults hit the observers' faces like windblown raindrops. These adults flew almost straight up without stopping in the trees, their flight was sustained from the moment of take-off to joining of the swarm above the tree canopy. The weather was now blustery, the large moving swarm was not going in any one direction but undulated and swirled in the air currents. There was a tremendous singing hum, varying in its intensity, like vibrating echoes. By now it was too dark to see in what definite direction, if any, the migratory swarm was carried. Probably it was carried some distance to the northeast since the wind was generally from the southwest at about 12 miles per hour. By $19^h05'$ all was quiet again and the wind had died down. Before I climbed down from the tree perch, small top swarms were forming over the branches of *Avicennia* and *Conocarpus* trees at an elevation of 25 feet. Flower feeding was again observed from $19^h07'$ to $20^h00'$ at the glade east of the marsh. Both sexes were now feeding at a greatly accelerated rate on both *Eupatorium* and *Bidens* flowers. No resting adults were left in the *Batis*. At $20^h00'$ a strong south wind developed and continued to blow from that direction most of the night.

By $12^h30'$ the next day, August 19, the water had receded from the marsh because the south wind had blown it northward upriver. The pupae left along the perimeter of the marsh were stranded among the windrowed mangrove leaves and on the mud in the trails. At $19^h10'$ the evening before numerous fish were taking their toll of the larvae remaining in the few puddles, and now none could be seen. The only evidence of the brood was a small emergence from pupae stranded among moist leaves. Some of these new adults were swept up and found to be almost all females, and it is interesting to note that they were smaller than the previous day's adults. Older adults from the previous day's emergence were feeding during the middle of the day ($12^h40'$) on the *Eupatorium* flowers.

Brood IV. Hob Horse Cove

This brood hatched September 9, 1956 and was just about as large as that produced in August, 1955. It was flooded in synchrony by high tide and rain in the same marsh as Brood III. The entire month of August had been extremely dry and adults from a July brood had oviposited millions of eggs over the entire area. On September 17–19 there were large emergences but twilight observations were prevented because of rains. On September 20 Messrs. W. L. Bidlingmayer, M. W. Provost, and the author observed a large departure of imagines from the *Batis-Avicennia* area located 200 yards west of the tall *Avicennia* zone to the east. We were trying to determine the direction the imagines would fly in relation to wind and also to get pictures of the departing migrants (see Fig. 3). The sky was entirely overcast and a light drizzle was falling during the observations.

At $18^h00'$, 21 minutes before sunset, the migrants started to depart in waves as already described for other exodi; they were leaving directly from the *Batis* as well as from a dead tree upon which many had climbed. The light intensity was low at an early hour because of the overcast weather; the temperature was 27° C. Most of the adults took off facing the wind but, since it was too strong for them to make headway, soon turned around and flew with it. At $18^h25'$ the initial departures were over, leaving great numbers of imagines resting in the *Batis;* most of these were apparently not old enough to leave. The wind was from the northeast at 3 to 5 miles per hour and the migrants traveled SSW, more or less with the wind. They attained altitude on an angle of approximately 45° from the point of origin and seemed to level off at about 20 feet elevation. At $19^h00'$ the air temperature was 26° C. It was decided to see if the imagines still remaining could be induced to depart from the *Batis* plants on which they were resting, by disturbing the plants. While Mr. Bidlingmayer was stationed 30 to 40 feet downwind Dr. Provost would periodically flush a host of adults—many of which would depart, flying downwind over Mr. Bidlingmayer's head at 8 to 15 feet elevation above the marsh. It was now $19^h15'$ and dark. Mr. Bidlingmayer's flash-light was shone upwards to intercept the imagines as they passed overhead. It was difficult to tell if many were flying at elevations higher than 15 feet. As they passed him, at this hour, he estimated that they were flying at angles between 16° and 20° from the point of take-off. A good many of the adults immediately returned to the *Batis* when disturbed. No mating was seen though it was not looked for specifically.

This was the fifth day of emergence and male swarms were over every small tree in the vicinity of the observation area. The air was literally teaming with mosquitoes when the electronic flash was shot skyward. These were flying, "milling around," even at 30 to 40-foot elevations.

Discussion

The work of the Entomological Research Center previously reported in quoted papers by Provost and Nielsen showed that *A. taeniorhynchus* was migratory during the early period of adult life. The combination of adult age and time of the day determined the time of migratory exodus from the breeding site. The observations reported in this paper have corroborated the previously published knowledge and added information on several points.

(1) Newly-emerged mosquitoes will feed on nectar before and during the ascent if such food sources are available. If nectar is not available, the exodus will take place anyhow but obviously a nectar meal before the exodus may have a considerable effect on the range of migration. The importance of carbohydrate food has been discussed by Hocking (1953), and it should be borne in mind that the reserves carried over from the developmental stages in the form of fat and glycogen are not immediately available for a migratory flight; only carbohydrates can be utilized for immediate use (Wigglesworth, 1950) while the mobilization of fat takes time. It is therefore reasonable to assume that mosquitoes have a much greater potential flight range when nectar is abundant at the breeding sites, as is the case during the flowering period of the black mangrove in spring and early summer.

(2) The second point of importance obtained from these observations is the increased knowledge concerning their sexual behavior. The concept previously arrived at—that females may copulate as soon as they can make extended flights (the copulation is always initiated in flight) and that the males are of a certain age before they can mate—also holds true with *A. taeniorhynchus.* During the several exodus periods described it was directly observed that a very large number of matings occurred in some cases, while in others there were few or none taking place. This may be explained by the presence or absence of males of sufficient age for copulation, e.g. with a hypopygial rotation of 135° (12–18 hours or even as young as 10 hours) (Nielsen, 1958).

(3) Nielsen (1958) pointed out that his observations only dealt with the habits of the animals up to the very point of exodus, when they disappear to a ground observer. During the observations reported here it has been learned that in some cases the potential migrants will remain flying around above the emergence site for some time after the exodus. This takes the form of a swarm-like flight which may be comparable to the "milling-around" before migration, known from the work by Gunn *et al.* (1945, 1948) and Kennedy (1951) on locusts and the butterfly *Ascia monuste* by Fernald (1937). Sometimes this "milling-around" is not visible from the ground but can be heard as a characteristic high pitched humming which can stop very suddenly as the animals disappear from the area. The author heard this on August 19, 1951 on Sanibel Island, and both saw and heard it on April 22 and May 21, 1953 on Sanibel Island and on September 20, 1956 at Hob Horse Cove. The conditions under which the "milling-around" occurs, during and after an exodus, are unknown.

(4) In other cases the migrants take off on a very determined flight with all animals flying in the same direction, this direction probably determined by wind. At low wind velocities (1/4m./sec. or less) the flight was oriented upwind; at higher wind velocities (1-1/2–2 m./sec.) the flight was downwind. There is a suggestion here of possible optomotor accommodation along the lines hypothesized for *Aedes aegypti* (Linnaeus) by Kennedy (1939).

(5) The exodi of April 22 and May 21, 1953, on Sanibel Island took place during dead calms and were oriented toward the sunset sky. This apparent visual orientation of exodi is reminiscent of locust orientation of swarm departures by the sun, when it is calm (Kennedy, 1951); the locusts, however, depart at 90° to the sun because that is how they orient to bask before the exodus, in other words, the orientation is not directly visual.

Summary

The flight behavior patterns of migrant *A. taeniorhynchus* during the exodus from the breeding sites are described for four large emergences.

It was found that feeding on nectar takes place before exodus if flowers are

present, and that matings occur during the exodus if males are old enough to copulate. Under certain unknown conditions the potential migrants "mill-around" high up in the air, both during and after exodus and presumably before the migratory flight begins.

The directional flight of the migrants was observed visually for the first time.

The direction of the departing migrants seems to be determined mostly by the wind, being upwind in wind velocities of 1/4 m./sec. and downwind in wind velocities over 1-1/2 m./sec.

In the one instance of the mosquitoes flying towards the sunset the weather was calm with no leaf movement at the top of the trees but it is not known if there were imperceptible air currents above the trees which influenced the flight direction.

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