ARTICLES

THE DISPERSAL OF *AEDES TAENIORHYNCHUS* I. PRELIMINARY STUDIES

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INTRODUCTION

The salt-marsh mosquitoes, *Aedes taeniorhynchus* (Wiedemann) and *A. sollicitans* (Walker), are among Florida's worst insect pests. They have been fought by organized districts since 1927, and in 1951 an estimated million and a half dollars were spent on their control. The biology of these mosquitoes, nevertheless, is largely unknown, particularly in their adult phase. Our dispersal studies are aimed not merely at establishing a "flight range" but more especially at elucidating the mechanics of such flights. The best hope for efficient control of these far-ranging insects lies in a thorough synthesis of their ecology, physiology, and group behavior. Concurrent research in all three of these phases is being carried on by the Division of Entomology of the Florida State Board of Health.

The first dispersion experiment with *Aedes taeniorhynchus* was made in August and September, 1951, on the coast of Lee County in southwestern Florida (Fig. 1). Sanibel is the southernmost of a chain of shell and sand islands extending along the western edge of the shallow bay at the mouths of the Peace and Caloosahatchee Rivers. This bay is roughly 10 by 30 miles, and almost in its center is Pine Island, 2 by 15 miles in size, and oriented along the same NW-SE axis. Bay shores in this area are typically mangrove swamps. The outer reef islands, like Sanibel, have mangroves on their bay sides and firm beaches on their Gulf of Mexico or seaward sides. The higher elevations (generally 3 to 10 feet) on the barrier islands are mantled with a scrub of shrubs and low trees. The interior of Sanibel

Island has many cordgrass (*Spartina bakeri*) sloughs and cabbage palm (*Sabal Palmetto*) groves. These abundant palms and the plantings of Australian pine (*Casuarina* sp.) constitute the major tree areas of Sanibel's interior. In the northwestern corner of the island there is a large key lime grove. And, of course, the entire bay (north) shore is covered with vast mangrove forests. The islands to the north along the reef—Captiva, Acosta, etc.—are very similar, though much smaller than Sanibel. By contrast, the mid-bay Pine Island is a strip of flat pine-woods much like the nearby mainland. It is completely encircled by mangrove swamps. The mainland on either side of the mouth of the Caloosahatchee River is flat pine-woods with a fringe of mangrove swamp. The bay waters are generally less than 8 feet deep and are sprinkled with mangrove islets. There is, however, a clear expanse of water at the nearest points between Sanibel and Pine Island (2 miles) and between Sanibel and the mainland (2½ miles).

Winds in this area at this time of year (cf. Table I) may be briefly described as follows: (1) pronouncedly eastern and averaging 3–6 m.p.h.; (2) on most days cyclonic disturbances occur in mid or late afternoon, with rain and winds shifting rapidly from all quarters and moving often at speeds up to 15 m.p.h.; (3) by sunset the atmosphere has usually cleared and east winds again prevail, although winds from the other three quarters may assert themselves until well after dark.

The work was centered on Sanibel Island, an area of prodigious *Aedes taeniorhynchus* production. The main objec-
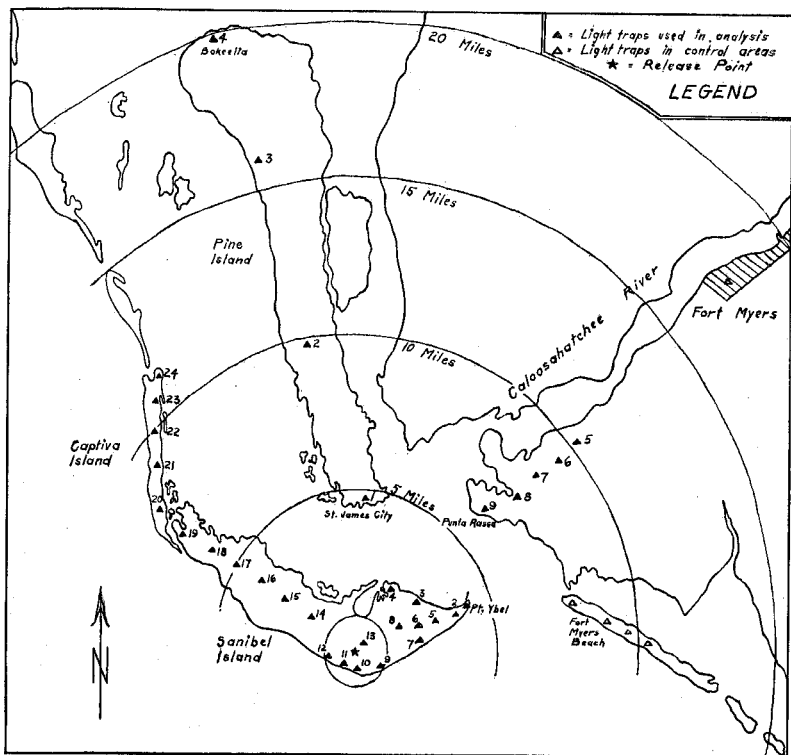
FIG. 1—The San Carlos Bay area, showing locations of light traps with respect to release point on Sanibel Island.

TABLE I. Wind direction at night in San Carlos Bay area at time of dispersal experiment.

Date and hours of night	Number of readings from indicated direction							
	N	NE	E	SE	S	SW	W	NW
Ft. Myers (U. S. Weather Bureau)								
Aug. 17–Sept. 20								
1800–2400	25	90	131	64	15	29	24	20
2400–0600	4	125	183	61	3	4	2	4
Aug. 19–Aug. 24								
1800–2400	2	18	22	6	4	7	7	0
2400–0600	0	9	45	4	1	0	0	0
Sanibel Island								
Aug. 19–Aug. 24								
1800–2400	1	3	8	7	1	1	0	0
2400–0600	0	0	1	1	0	0	0	0

tives were to familiarize ourselves with the radioactive isotope marking technique, with the various adult collecting techniques, and with the necessary statistical techniques. The secondary objective was to get some preliminary idea of what to expect by way of dispersion pattern. The technique findings will appear in another paper; the present paper will discuss only the data obtained on dispersion.

Hatching of *Aedes taeniorhynchus* eggs in the San Carlos Bay area is dependent on rains, high tides, or combinations of both. Six large broods occurred in 1951. The first three were strictly tidal in origin and emerged approximately on April 30, May 29, and June 26. Simultaneous heavy rains and high tides, July 18 to 23, gave rise to the largest brood of the year, in early August. Remnants of this brood were still on the wing during the early days of the dispersal experiment. The heavy rains of August 12–13 produced the first major hatch in the interior sloughs of Sanibel Island; this is Brood I of the experiment interval, and the marked mosquitoes were of this hatch. Very heavy rains on Aug. 21–22 produced an even larger hatch in interior sloughs of the entire bay area; this was Brood II of the experiment interval. These two rain-produced broods (I and II) apparently exhausted the supply of conditioned eggs in the entire area, for the torrential rains of mid-September and early October failed to produce any further large broods. The synchrony between the unmarked and marked populations during the experiment is shown in Fig. 2.

METHOD

Larvae were collected from a rain-filled slough and transported in metal drums to wooden tanks at the release point two miles away. The number of larvae in each drum load was computed from 10 ml aliquots. As the four wooden tanks were being filled, larval densities were again computed. Approximately three million third and fourth instar larvae were in the tanks when the isotope was introduced.

The marking technique employed was essentially the same as that used by Thurman et al. (1951). The larvae were concentrated in wooden troughs and the P^{32} introduced into the water as an H_3PO_4 solution. The P^{32} was supplied by Tracerlab, Inc. on allocation from the Isotopes Division, U. S. Atomic Energy Commission. The dosage of isotope in all four tanks was .019 μc per larva. However, since the larval density varied among the tanks from 3.6 to 5.4 per ml, the rearing solution varied from .066 to .101 μc per ml.

As soon as pupae appeared, the 3' x 6' tanks were covered with 3' x 6' x 1½' screened cages in order to retain the adults for simultaneous release. The isotope was introduced in the afternoon of August 16, and the main emergence took place half an hour before sunset on August 19.

A minor release was made on August 18; there were certainly some escapes before then, and a small number left the tanks after the 19th. Although the numbers leaving the tanks within 24 hours of the big simultaneous release of August 19 are uncertain, there is yet no doubt about the overwhelming numbers having been released at the given hour. Attempts to compute per cent emergence failed; there was a very substantial mortality, larval and pupal, in every tank. The release can be given only as approximately one million adults, at least 75% of which left the site half an hour before sunset on August 19.

Four methods were employed for recapturing the marked (radioactive) adults. (1) Thirty-nine New Jersey light traps were operated nightly from five days previous to thirty days after the release; their distribution is indicated in Fig. 1. (2) Two trucks equipped with cone-traps on fender and over cabin roof were operated over set routes three round trips per night for five nights following the release. (3) Aspirator (biting) collections were made at 39 stations, three times at night and three times in the daytime, for six days following the release. (4) Sweep-net collections were made at the same 39 stations on the same schedule. Standard and rigid
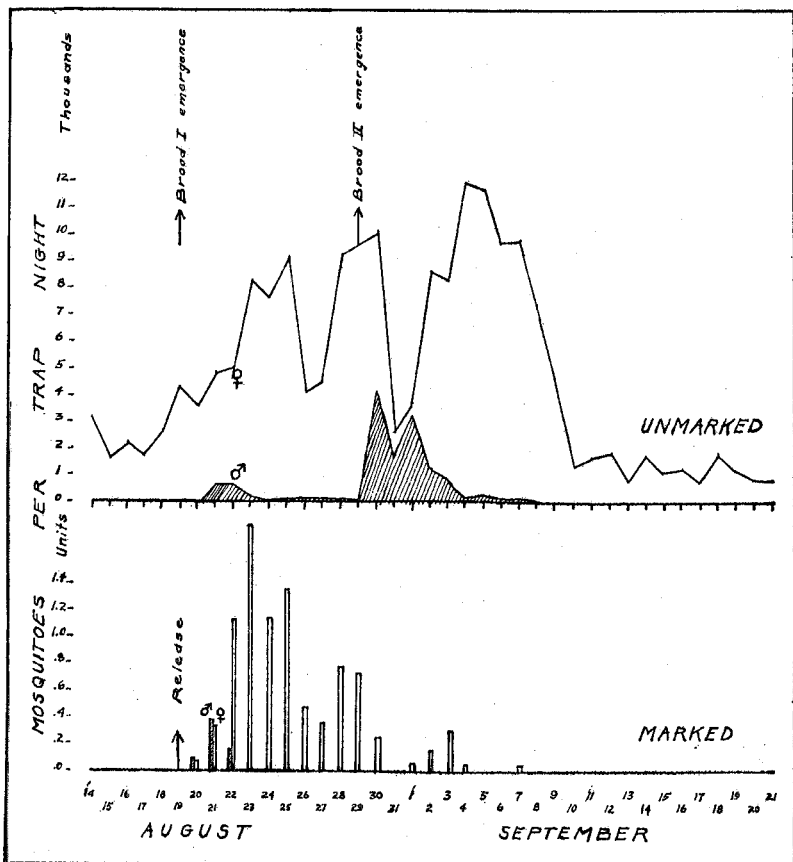
FIG. 2—The relation of the marked brood of *Aedes taeniorhynchus* to the unmarked population. Both graphs based on averages of 33 light traps in the San Carlos Bay area.

procedures and schedules were maintained for each type of collecting. The light traps were concentrated within five miles of the release point, but extended out to 20 miles. The truck trap routes extended four miles from the release point and were each divided into 10 linear portions. The sweep-net and aspirator stations extended out 7 miles from the release point in as uniform a pattern as the terrain and its accessibility permitted. Because of the operating limitations of each type of collection, it was impossible to establish a strict geometrical distribution of recapture points.

All collections were monitored with a laboratory type Geiger-Mueller tube and counter. This was done as quickly as the laboratory force on Sanibel Island could handle the collections. Marked mosquitoes were metered (in counts per minute), sexed, and counted at once. The negative (non-radioactive) portions of collections were set aside for identification, sexing, and counting as time allowed. This latter chore was not completed until February, 1952.

The 10 days of intensive work on Sanibel employed 20 people full time and 6 part time. The light trap work employed two of these an additional three weeks, and

the laboratory work kept three persons occupied some six months.

RECOVERIES OF MARKED MOSQUITOES

1. Light Traps

Radioactive mosquitoes were recovered largely from light traps. Although one of the four traps at Fort Myers Beach did yield one marked female, on August 28, the total collections from these traps, from the Fort Myers trap, and from the trap at Bonita Springs were all extremely small when compared to the other traps used in the experiment. These six traps were in areas of adulticiding control, but whether or not this explained the small collections, it is felt best to restrict our analyses to those traps which all fell within the same performance pattern and where there was no possibility of control interference. The 33 remaining traps, during their 39-day runs (1220 collections) collected 5,986,014 female and 483,661 male *Aedes taeniorhynchus,* for a per-night, per-trap average of 4907 females and 396 males. For the period during which marked mosquitoes entered the traps (Aug. 20 to Sept. 7), 4,610,289 females and 473,344 males were collected, for a per-night, per-trap average of 7546 females and 775 males. In all, 288 marked females and 19 marked males were captured.

A. Females

Distance.—Marked females were caught at the farthest trap operated, 20 miles from the release point (Table II). The largest returns were at traps 9 to 11 miles away on Captiva and Pine Islands. Unfortunately, there were few traps beyond ten miles. Within ten miles of the release point, there was a decrease in number with distance in a northeasterly direction, but an increase in north and northwesterly directions (Fig. 3). The 5 traps within one mile of the release point differed from the two traps 16 and 20 miles away on Pine Island not so much in size of marked-female collections as in their continuity where the distant traps were discontinuous in their returns. All these facts suggest that marked females may have gone, in substantial numbers, beyond the 20 mile limit set by traps.

Direction.—Except for the eastern half of Sanibel Island, where power lines permitted a scattered distribution, the light traps were arranged primarily along three radii from the release point. The northwestern radius followed the outer islands to the northern tip of Captiva. The northern radius crossed Tarpon Bay and up the whole length of Pine Island to Bokeelia at its northern tip. The northeastern radius went to the eastern tip of Sanibel, then across San Carlos Bay, up the road from Punta Rassa on the mainland to Fort Myers. The traps along the northwestern and northern radii caught more marked females than those in a northeasterly direction (Fig. 3). It is particularly noteworthy that the nearest trap on the mainland (6 miles northeast of the release point) is the only one of the 33 traps which caught no marked mosquitoes at all.

Time.—Marked females were caught in light traps from the 1st to the 19th days following the release. The decrease in numbers with time was not constant (Fig. 4). The time distribution showed a very marked cycle with peak catches of 58, 27, 10, and 1, on Aug. 23 (4 days after main emergence), Aug. 28 (5 days later), Sept. 3 (6 days later), and Sept. 7 (4 days later). The same periodicity showed up when the various light traps were grouped according to either distance or direction. This remarkable phenomenon is discussed later.

B. Males

One marked male was caught in a trap two miles northwest of the release point; the remaining 18 were caught in the five traps between ¼ and 1 mile from the release point (Table III). Within such a short distance, direction was irrelevant. In point of time, 3, 12, and 4 respectively were caught on Aug. 20, 21, and 22, or 1, 2, and 3 days after the main emergence.

2. Truck Traps

During their 6 days of operation, the truck traps collected 33,259 female and

TABLE II. Light trap recaptures of marked female *Aedes taeniorhynchus* in first dispersal experiment. In the first column the letter designations are: S, Sanibel Island; C, Captiva Island; P, Pine Island; M, Mainland. X indicates trap did not run.

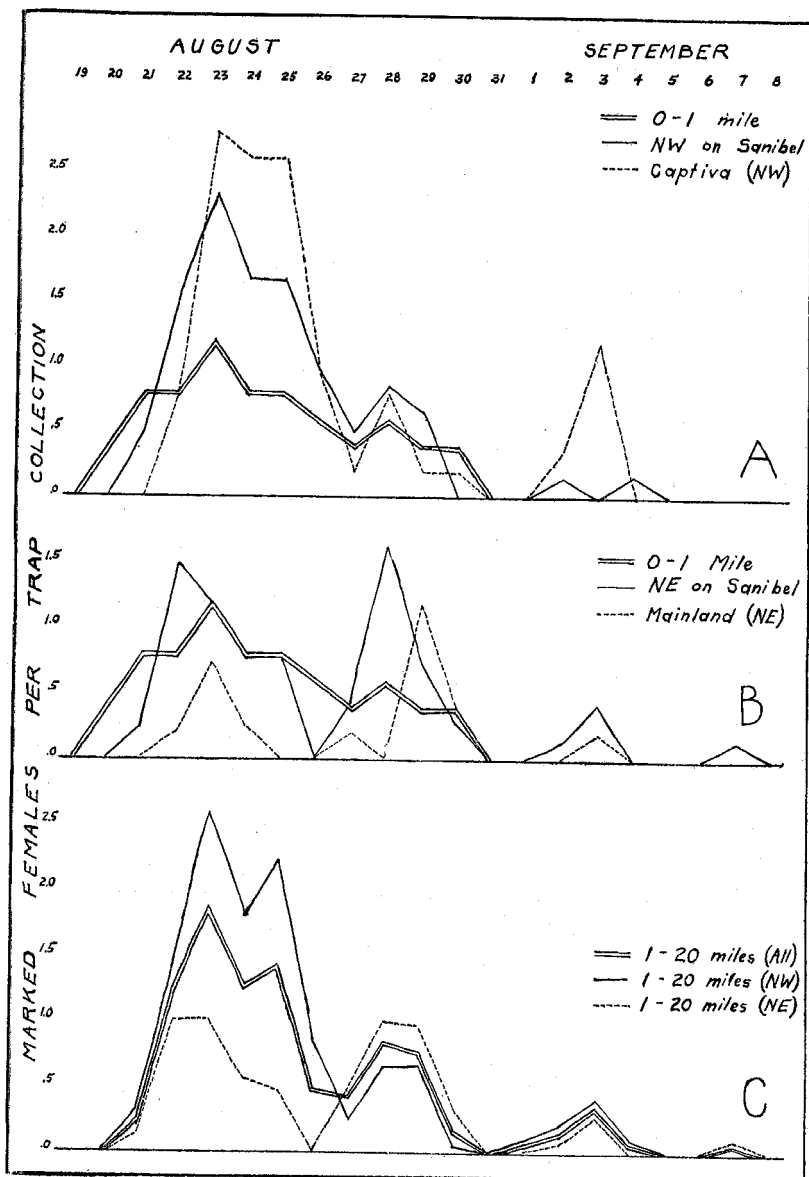| Trap Number	From Release Point Miles	Direction	Marked females caught in August-September: 20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	Total
S 13	.3	N	1	1	1	5		1	2		1		1									13
S 10	.6	S		2	2		2					2		x								8
S 9	.8	SE									1											1
S 11	.8	SW	1		1	1		2	1		1		1									8
S 12	1.0	SW		1			2	1			2											6
S 8	1.6	ENE	1			1	2	1	1	2	1		1									8
S 14	2.1	WNW			2	1	1	2			2											6
S 7	2.2	E		1			1	2			2											5
S 6	2.6	ENE			3	1		2		3	3	x					2					10
S 5	2.7	ENE			2	2		2	x			2							x			10
S 4	2.7	NNE		1	2	4	2	2			6	3	1									21
S 3	3.0	NE														1						3
S 15	3.1	WNW				1	1					1										2
S 2	3.9	ENE			2	1	2		2	x		1	1									4
S 16	4.1	WNW				1	1				1		1									3
S 1	4.4	ENE			2	1	1	1		2	4	1					1					9
P 1	4.3	N		1	1	1			2	2	1	2				1		1				4
S 17	5.1	NW			7	4	2	4														26
M 9	6.0	NE																				0
S 18	6.1	NW	1		x																	9
S 19	6.9	NW				2	3	3	4	1	1	1				1						20
M 8	7.0	NE				6	3	3	x	1	1	2	2			1						9
C 20	7.6	NW				3					1	1					1					3
M 7	8.0	NE					1	1														1
C 21	8.6	NW				2	5	1	3													3
C 22	8.9	NW				8	1	3														20
M 6	9.1	NE					3	1									1					1
P 2	9.7	N		1	7	8	7	8	1													32
C 23	10.0	NW			4	2		4	2	1	3	4	1			1	5			x	x	29
M 5	10.4	NE			1							3				1						4
C 24	11.0	NW				2		4	x	1	3	1		x	x	1						9
P 3	16.0	NNW				2		1							1							3
P 4	19.8	NNW					1	1	x	x	1										1	4
Total (33 traps)			2	10	37	57	38	44	15	10	26	23	7	0	1	4	10	1	0	0	1	286

Fig. 3—Comparisons of light attraction periods of marked females as reflected in light trap recaptures.

8,432 male *Aedes taeniorhynchus* in 735 collections. Of this number, 8 females and 1 male were marked (Table IV). The single male capture was at a point on the Gulf beach ¾ miles south of the release point at 0400 on Aug. 24 or five days after the big emergence. Five of the 8 females were caught during the night of Aug. 20–21, three within ½ mile either north or south of the release point and two somewhere between ½ and 2 miles distant, one northwest and the other northeast. One female was caught at 2300 on Aug. 21 within ½ mile of the release point (north or south), and two were caught at 2300 of Aug. 22 somewhere
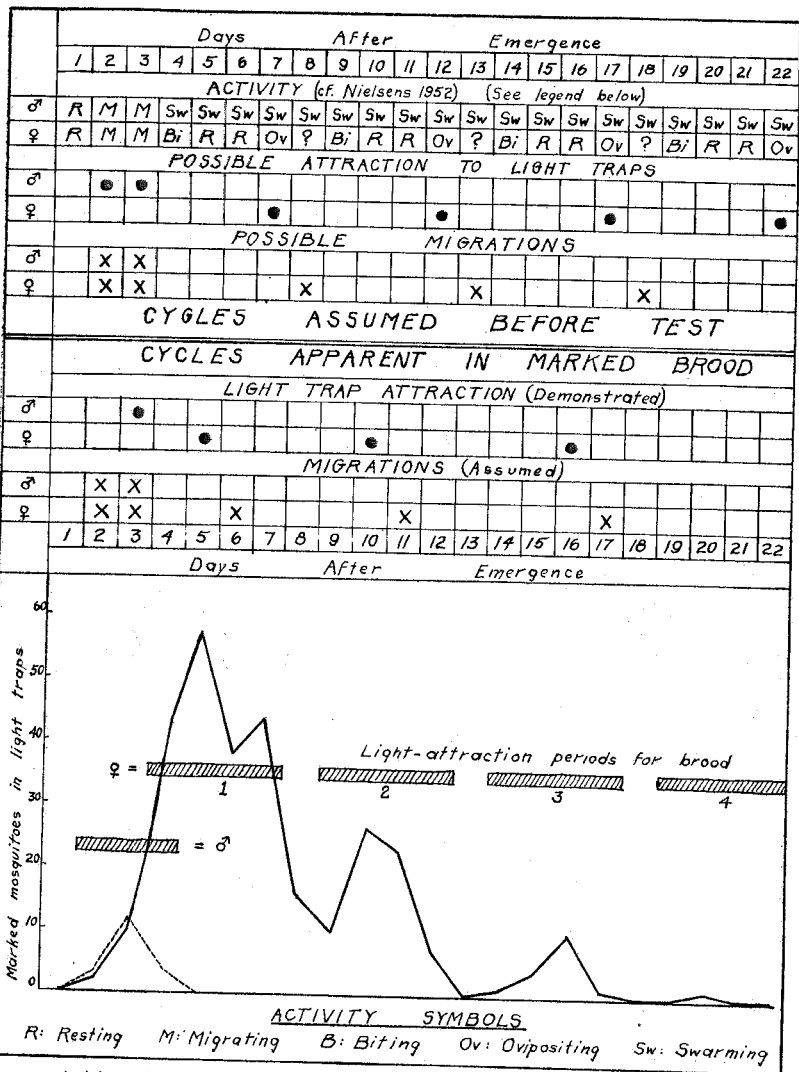
Fig. 4.—Activity cycles of *Aedes taeniorhynchus*, as hypothesized by the Nielsens (1952) and as revealed by the dispersal experiment.

TABLE III. Light trap recaptures of marked male *Aedes taeniorhynchus* in first dispersal experiment. All were on Sanibel Island.

Trap Number	From Release Point		Date in August			Total
	Miles	Direction	20	21	22	
S 13	.3	N	1	1		2
S 10	.6	S		3	1	4
S 9	.8	SE		1		1
S 11	.8	SW	1	6	2	9
S 12	1.0	SW	1	1		2
S 14	2.1	WNW			1	1
		Total	3	12	4	19

between 2 and 4 miles northeast of the release point.

3. Sweep-Net Collections

The 39 sweep net stations during their week of operation yielded 9,651 female and 426 male *Aedes taeniorhynchus* in 1033 collections. The only marked mosquitoes caught were two females at 1011 on Aug. 21, ¾ miles southwest of the release point and one female at 0847 on Aug. 19, one mile west of the release point. It is noteworthy that this latter mosquito was caught 10 hours before the main release.

4. Aspirator Collections

The same 39 stations yielded 1049 collections to the aspirator for a total of 13,906 females and 37 males, the latter accidentally having rested on the bodies of the collectors. The only marked mosquito thus caught was a female at 0810 on Aug. 23 at a station 7 miles northwest of the release point.

5. Miscellaneous Collections

A few male swarms were collected by sweep net, but the relatively small samples yielded no marked mosquitoes. Five light traps were experimentally operated without lights, paired with the standard traps within a mile of the release point. The "blind" trap ¼ mile northeast of the release point caught one marked female on Aug. 22, and the "blind" trap one mile southwest caught a marked female on Aug. 23. The laboratory and headquarters for the experiment were at the lighthouse station at the eastern tip of Sanibel Island. Mosquitoes gathered in considerable numbers on the white building and a few sweeps under the high eaves with a sweep net (on the end of a bamboo pole) between 0115 and 0200 on Aug. 24 yielded 16 male and 13,801 female *Aedes taeniorhynchus*. Two females were radioactive. This was 4¼ miles east of the release point.

TABLE IV. Truck trap recaptures of marked *Aedes taeniorhynchus* in first dispersal experiment.

Time		From Release Point		
Date	Hour	Miles	Direction	Sex
Aug. 20	2300	0.0–0.5	N or S	Female
,,	,,	,,	,,	,,
,,	,,	,,	,,	,,
Aug. 21	0400	0.5–2.0	NE	,,
,,	,,	,,	NW	,,
,,	2300	0.0–0.5	N or S	,,
Aug. 22	,,	2.0–4.0	NE	,,
,,	,,	,,	,,	,,
Aug. 24	0400	0.6–0.8	S	Male

DISCUSSION

Dispersion and migration in insects have been so diversely interpreted that the two terms mean little without definition. In the mosquito field, this is traceable to the universal prompting to consider migration merely a matter of long distances being covered. The only hope of bringing order to our terminology lies in examining the objective causality, or ethology, of flights resulting in dispersion,—dispersion meaning according to the dictionary, simply "distribution from a fixed source." Dispersion results whenever a member of an insect population takes wing. While resting, that insect may be in any of several physiological states and this state will determine its reflex response to any external stimulus. Those physiological states characterized by a neural unbalance or unsatisfaction (e.g. hunger, thirst, rut) are accompanied by an appetence: an active seeking of the external stimuli associated with the satisfaction of the physiological want. Flight impelled by appetence, we may call *appetential* flight. It receives internal direction, whatever may be the influence of external stimuli. The insect, nevertheless, cannot be constantly under the nervous tension of a physiological need, so that there must be a physiological state of satiety which from the standpoint of reflex possibilities for that insect would be strictly a neutral state. While in this state, the insect is still sentient, of course. Since, however, there is no appetence, responses (if any) to external stimuli will be purely mechanical and with external direction only. Should any external stimulus cause an insect in a neutral state of rest to fly, the result will be a *non-appetential* flight. Such flight is without internally influenced orientation. We believe that insect migrations are examples of non-appetential flight, a special flight which serves no special physiological need, whatever teleological end it may subserve.

Tinbergen (1951) in his excellent synthesis of innate behavior appears to infer that the flow of motivational impulses through the nervous system is continuous so that an animal at all times must be either behaving "appetitively" * or consummating the act resulting from such behavior. "In extreme cases the appetitive behavior may be prolonged and highly adaptable, as in the migratory behavior of animals" (p. 105). Since appetential behavior is admittedly purposive, Tinbergen is in opposition, at least as far as insects are concerned, to Uvarov (1928), Kennedy (1951), and others who insist that insect migrations are not directed to a goal.

Appetential flight (e.g. search for food, shelter, mates, oviposition sites, etc.) will necessarily result in a certain amount of dispersion. This type of dispersion is common to all mosquito species since it reflects flight activity incidental to the satisfaction of the biological needs of a lifetime. A multitude of appetential flights enters into the ultimate dispersion of a population originating at one point. So diversified and numerous, indeed, are these flights that the resulting "normal" dispersion will be random, omnidirectional, and with limits a function of (1) density at the source, (2) longevity, (3) average length of component flights. The pattern of this normal (for want of a better word) dispersion may be affected by the distribution of shelter, food, etc. and possibly also by weather, but on the whole it tends to be radial with the distribution along any radius typically a hyperbolic regression. It must be noted, however, that there are long appetential flights of a special nature which should not be confused with true migration; a classic example would be the hibernational flights of many anopheline species.

In such a species as *Aedes taeniorhynchus,* migrational flight effects a dispersion which must be superimposed on the normal dispersion resulting from appetential flights. The ultimate distribution or dispersion of a population of migratory mosquitoes may be determined

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* According to dictionary, "appetitive" and "appetitively" are derivatives of *appetite.* Since we are concerned here with *appetence* (also in dictionary), the derivatives thereof should be "appetential" and "appetentially."

more by a single flight participated in by all individuals than by the subsequent multiplicity of appetential flights performed individually. Such factors as density at the source and longevity, which have much to do with setting the limits of normal dispersion, probably have very little effect on migratory dispersal limits. Conversely, weather and topography may exert the major influence on orienting or channeling migratory flight, and hence may be the most important determinants of the dispersion pattern for a population of migratory mosquito species. It follows, therefore, that for non-migratory mosquitoes the pattern and limits of dispersion will be set largely by biological needs of the insects, whereas for migratory mosquitoes they will be determined largely by meteorological and topographical accident.

Assuming that "flight for flight's sake" is the cause of a special migratory dispersion in some mosquito species demands some sort of explanation. It is suggested that both males and females of *Aedes taeniorhynchus* respond to an undefined light factor at dusk and dawn (for discussion with respect to male swarming, cf. Nielsen and Greve, 1950) by ascending from their resting places and flying. These are the primary, non-appetential responses, common to both sexes, in reaction to the same stimulus. Physiologically, this flying is non-motivated and non-purposive. Once on the wing, with no internally orienting influences of the appetential type, the direction of their flight will be determined by purely external factors. Migration then ensues as a flight in which the orientation of the insects' bodies, specifically, is non-purposive and at the mercy of external stimuli.

This secondary effect, migration, may be modified or arrested but the primary response, flight, is presumed to occur every dawn and dusk as a robot phenomenon. Newly-emerged adults may delay their primary response beyond dusk if they have not by that time attained an age at which sustained flight is possible; i.e., the exodus may occur at any hour of the night. In females the secondary effect may be arrested by heaviness of abdomen as a result of a blood meal or gravidity. Since these circumstances endure perhaps three consecutive days, migrations beyond the initial exodus from the emergence site would occur on a five-day cycle, i.e. during the permissive interval between oviposition and the next blood-meal (Fig. 4). In the case of males, it is necessary to consider the possible intervention of appetential behavior. It is conceivable that males accompany females in the initial exodus merely because the primary response is at once diverted into a mating pursuit of females. This would be the mass counterpart of individual males dropping out of swarms, later in life, to copulate with females flying nearby.* Since later female migrations are not mass phenomena exerting a mass stimulus, the males perform no further migrations but swarm every twilight the rest of their lives, as observed by the Nielsens (1952), with copulation accidental only since nearly all females have been impregnated during the initial exodus. It is furthermore conceivable that the swarming of males as well as the strange oviposition flights of females described by the Nielsens (1952) may be diversions of the secondary effect consequent upon fulfillment of the same primary response hypothecated for both sexes.

The findings of any dispersion experiment are completely at the mercy of the sampling techniques used, both in collecting mosquitoes for marking and in collecting them later for re-identification. In the case of *Aedes taeniorhynchus,* for instance, marking and releasing mosquitoes caught by light trap or bait trap would yield a most untrue picture of dispersion from breeding areas if it happened, as appears to be the case, that the main migratory flight occurs before the animals start the blood search and before they can react positively to light. This bias was avoided

* Mating in swarms was first observed for *Aedes taeniorhynchus* by Mr. James S. Haeger on Sanibel Island, Florida, December 3, 1951. It never occurred in the swarms which the Nielsens observed so closely in the Fort Pierce area in 1951.

in this experiment by marking the insects in the aquatic stages, thus enabling a tracing of their dispersion back to a true and natural origin in both time and space. This elimination of bias is not achievable in sampling the population for recaptures. For *Aedes taeniorhynchus,* and certainly for many other mosquitoes, there is no collecting technique known which will sample the entire population. All methods are selective: light traps sample that segment of the population which is on the wing and responding positively to light, bait traps or biting collections sample only that population segment (all female) which is at the time searching for blood, nets of any kind sample only those segments of the population which are either on the wing at the time or resting in the type of vegetation swept at the time, and so on. Interpretation of recaptures in a marking-releasing-recapturing experiment must therefore conform to the techniques employed in recapturing. Although we tried in this experiment to employ a variety of recapturing techniques in order to circumvent sampling selectivity, it developed that only the light traps yielded significant numbers of recaptures. Interpretation of our findings is consequently inseparable from an understanding of the light trap reactions of *Aedes taeniorhynchus.*

1. Females

The most significant finding of this experiment was the periodicity of marked female numbers in the light traps. On the basis of phototaxis studies in the laboratory and visual observations in the field, the Nielsens (1952) have advanced the working theory that in *Aedes taeniorhynchus* the females react positively to light approximately on their seventh day of adult life and cyclically about every fifth day thereafter. Except for the initial light attraction being two days earlier, our dispersal study contributes striking confirmation of this theory (Fig. 4). From the standpoint of light trap analysis, it is now fairly certain that female numbers must hereafter be interpreted with this phe-

nomenon in mind. Studies in progress will clarify the rigidity of the gonotrophic cycle, but it is obvious even now that for a brood of *taeniorhynchus,* the overlap of individual light attraction cycles will result in a *light trap number* x *time* distribution with a wave pattern reflecting the degree of isochronism in the emergence.

Interpretation of light-trap data on female *taeniorhynchus* is further complicated by the migration periods. The Nielsens (1952) give convincing evidence that "dispersal" (= migration, in our sense) occurs sometime between the first and fourth days of adult life,—previous to the onset of biting activities and to the first light attraction period. They found biting activities to be concentrated on a five-day cycle,—4th, 9th, 14th, etc. days after emergence, while ovipositing followed the same cycle three days later,—7th, 12th, etc. days after emergence. They do not, however, discuss the possibility of migratory flights occurring also every five days, say, on the 2nd, 8th, 13th, etc. days of adult life. In the experimental results under discussion, the fact that traps in a northeasterly direction collected as many marked females in the second light attraction period as in the first, while traps to the northwestward collected far more in the first than in the second (Fig. 3-C) suggests that a migration may have taken place in the early days of each gonotrophic period. The odd pattern on Captiva Island (Fig. 3-A) with the third period bringing in more marked mosquitoes than the second, although a full six days of progressive mortality intervened, seems also to indicate brood shifts at each period. The same applies to the pattern at Sanibel trap #4 (2.7 miles NNE) where the second period brought in more marked females than the first, the third none at all, and the fourth one single mosquito. If there were no further migrations after the initial one, the basic dispersal (non-appetential) would be ended before the first light attraction period and the distribution essentially the same for all light attraction periods. Consequently, the pattern shown at the bottom of Fig. 4 for all

recaptures, with each successive modulation smaller than the previous one in accord with mortality rate, would prevail at each trap location or group of locations. This definitely was not the case.

The two concepts of female *taeniorhynchus* migration that have been discussed, periodicity and non-purposiveness, lead to an entirely different dispersal pattern from any discussed in the voluminous literature on mosquito dispersal, although results obtained by Clarke (1937, 1943) and Horsfall (1942) with other migratory species (*Aedes vexans* and *Psorophora confinnis* respectively) resemble ours on several points. It is a pattern of random dispersal (appetential) periodically repeated from foci established by the preceding migratory dispersal (non-appetential), —all very likely conditioned by meteorological and topographical exigency. Since the latter circumstances may vary at each migration, the net dispersal for a brood is not only very complex but infinite in its possibilities. The one dispersal pattern rendered impossible is the purely radial type with densities a simple function of distance from point of origin.

With such a dispersal pattern, the area of occupancy by a brood from a single origin would, in the absence of weather or terrain influence, expand cyclically. The density of mosquitoes at each expanding perimeter would be decreased according to a calculable regression which would be a function of the longevity factor and area factor. If the entire brood were to align itself evenly along the ten mile perimeter after the first migration, the second 10-mile migration would bring 3.2% of the original brood back to within a mile of the point of origin. This figure, of course, assumes no mortality, no weather deflection, and 100% migration. The return to origin would result in approximately the same density within a mile of the origin during the second light attraction (= oviposition) period as prevailed within a mile of the 10-mile perimeter during the first oviposition period. What is more likely than an alignment on any perimeter, however, is a radial distribution on a normal (probability) curve with a peak, say, at the 10-mile perimeter. Since area on any perimeter is inversely proportional to the radius, the actual distribution of mosquito densities would be shifted somewhat to the origin side of the maximum. Thus, if the mean distance of a migration were 10 miles, the density on the 5-mile perimeter would be 2/3 that on the 10-mile perimeter (probability curve factor x area factor, 1/3 x 2) while on the 15-mile perimeter the density would be 2/9 that on the 10-mile perimeter (1/3 x 2/3).

For the first light attraction period of the marked brood, the light trap recoveries appear to fit roughly into such a curve. It is clear, however, that any shift in dispersal resulting from meteorological or topographical influences could alter these density proportions. The data indicate a northwestward shift of this nature, which could well account for the presence of marked females close to the release point,—for theoretically none should linger here during the first light attraction period.

At this point it would be well to emphasize that random, omnidirectional dispersion of the type hypothesized above has not been demonstrated for *Aedes taeniorhynchus*, even as a primary trend subject to later deflections by weather or other factors. Field observations on several occasions have shown rather a unidirectional exodus, and it is highly probable that winds and topography exert a channeling effect on the migration. Although the directional data from the present experiment are definitely prejudiced by the distribution of light traps, the fact remains that the traps in a northeasterly direction yielded only a fraction of the returns produced in the traps to the north and northwest at any distance, on or off Sanibel Island (Fig. 3). This northwestward deflection may have resulted from either a meteorological influence, the prevailing southeasterly winds (Table I), or a topographical influence, the alignment of the coast and islands, or a combination of both.

The fact that *Aedes taeniorhynchus* rarely occurs in nuisance proportions more than five miles inland from tidewater (Provost, 1951) in spite of its now demonstrated much longer flight range is itself evidence that migrations must largely parallel the coastline. This fact in conjunction with the repetition of migrations by the same brood could well result in oviposition (in second or later periods) at the site of origin in spite of the remarkable exodus soon after emergence.

2. Males

It is usual with light trap catches of *Aedes taeniorhynchus* for females to outnumber males by a considerable margin. It is absolutely essential that the reasons for this be understood before any male light trap data are interpreted. We must digress here to prove our points: (1) positive phototaxis is as strong in males as in females, (2) female collections average larger than male collections because the larger ambit of appetential flight activity, in place and in time, brings more of them within the orbit of light trap attraction, and (3) large male collections are purely a matter of chance concentrations at the trap site.

The history of *Aedes taeniorhynchus* light trap captures in Florida reveals that females exceeded 100,000 in a night's collection once (265,000) and males did it twice (117,000 and 125,000). Obviously there are circumstances under which males will come to traps in as large numbers as females do. In the course of the experi-

ment, the five light traps within a mile of the release point were paired with "blind" traps, i.e. regular light traps run without a light; the two traps were 20 feet apart at each location. The blind traps caught only a fraction of what the lighted traps caught. It was found (Table V) that the preponderance of females over males was almost invariably greater in the unlighted than in the lighted traps. During the peak days following the two big emergences of the experiment interval, the female to male ratio averaged 2.4 times as great in the unlighted as in the lighted traps. This would certainly indicate that, *at the trap site,* males were attracted to light as much or very likely more than females. We have on record hundreds of collections in which males far outnumbered females.

An analysis of large collections of either sex from the San Carlos Bay area (Table VI), 1946 to the present experiment, reveals that as the size-of-collection category increases, the ratio of female to male collections within these categories decreases. Collections of over 50,000 are about equally divided between the sexes, but as the size diminishes the ratio of female to male collections increases until it reaches approximately 10:1 for collections between 5,000 and 20,000. It is plain, therefore, that more females than males are caught in light traps not because female collections are larger but because large collections of females are more frequent. The sedentary nature of post-migration males compared with females would result in the traps sampling much larger segments

TABLE V. Sex ratios of *Aedes taeniorhynchus* caught in New Jersey traps with and without light at five locations on Sanibel Island, August 21–26, and Aug. 30–Sept. 7, 1951.

Trap number	Average per trap night				Female/male		Light attraction male>female
	trap with light		trap without light		light	no light	
	female	male	female	male	1	2	2/1
9	3,709	1,297	78	15	2.86	5.20	1.82
10	5,954	779	206	5	7.64	41.20	5.39
11	7,580	2,193	389	42	3.45	9.26	2.68
12	2,887	889	178	42	3.25	4.23	1.30
13	14,173	1,544	764	26	9.17	29.38	3.20
Average	6,928	1,354	324	26	5.11	12.46	2.44

TABLE VI. Analysis of *Aedes taeniorhynchus* light trap catches exceeding 5000 in either sex, San Carlos Bay area, Florida. A = semi-weekly catches, 1946 to Aug. 14, 1951. B = daily catches Aug. 14 to Sept. 21, 1951. C = daily catches during first light-attraction period of Brood II, Aug. 29 to Sept. 4, 1951. D = daily catches during first light-attraction period of Brood I, Aug. 20–26, 1951. The marked mosquitoes of the dispersal experiment belonged to Brood I (column D).

| Size of catch in thousands | Number of Collections | | | | | | | | Ratio of female collections to male catches in each size | | | |
| | Females | | | | Males | | | | | | | |
	A	B	C	D	A	B	C	D	A	B	C	D
5–10	103	218	60	52	10	9	8	1	10.3	24.2	7.5	52.0
10–15	52	91	29	28	5	4	3		10.4	22.8	9.7	—
15–20	13	48	18	11	1	2	2		13.1	24.0	9.0	—
20–25	8	16	10	3		1	1		—	16.0	10.0	—
25–30	9	14	3	4	2	2	2		4.5	7.0	1.5	—
30–35	5	2	1		1				5.1	—	—	
35–40	3	2	2						—	—	—	
40–45	5								—			
45–50	2	1	1		1				2.0	—	—	
50–55	1	2			1				1.0	—		
55–60												
60–65	1								—			
65–70	2				1				2.0			
70–75	1								—			
75–80												
80–85	1				1				1.0			
85–90		1								—		
90–95												
95–100					1				*			
100 +	1				2				2.0**			
Total	207	395	124	92	26	18	16	1	8.0	22.0	7.8	98.0

— = Only female collections.
* = Only male collection.
** = Reversed ratio, i.e. male to female.

of the female population than of the male, and this is a more plausible explanation of female preponderance in traps than the assumption that light attraction *per se* is stronger in females.

Through most of their post-migration lives, males are so highly sedentary (cf. Nielsens, 1952) that large collections such as are given in Table VI may be purely accidental, i.e. there just happened to be large concentrations of migrating males at the immediate site of the trap. Some evidence for this is found in the fact that these large male collections are more localized than large female collections; for instance, of the 26 collections in the first male column of Table VI, 22 were at one trap and this included all those of over

20,000, and of the 18 large male collections made during the dispersal experiment, 12 were at 5 of the 33 traps.

It is possible therefore to explain the small number of male recaptures in this experiment on the assumption that the males of this brood just did not happen to be concentrated at the trap sites on August 20–22. This assumed behavior among the marked males is corroborated among the unmarked males of the same brood. The males of Brood I (emerging Aug. 18–19) simply did not enter traps as did those of Brood II (emerging Aug. 29–31). The difference (Table VI), however impressive for the entire trapping record of the experiment, was nevertheless attributable to but a few adjoining traps

(chiefly Sanibel Nos. 14, 15, 16, 17) and can therefore be explained as a matter of chance concentrations of migrating males at trap sites.

The limited light trap recaptures (19 vs. 288 females) need not be attributed to a biased sex ratio at release. Estimates at that time, if anything, favored males. Both the short duration (3 days) of marked male recapturing and the short distance (2 miles) involved must be interpreted in the light of factors discussed above.

On the point of longevity, the Nielsens (1952) have demonstrated that the swarming period of males extends from "the age of 4 days until they are 2–3 weeks old." The disappearance of males from light trap collections at the age of 4 days in this experiment suggests that (1) they are not attracted to light during the swarming period of their lives, or (2) they are so sedentary during this period as not to even approach the vicinity of traps. The observations of the Nielsens substantiate both of these possibilities. Since the light trap history of *taeniorhynchus* abounds with a sprinkling of male captures long after main emergences, it is extremely difficult to believe that males are never attracted to light beyond their fourth day of adult life. It is more likely that between swarming intervals, i.e. in the middle of the night, they may be positively phototactic but seldom occur in traps because of their extreme sedentariness at this age.

It appears, therefore, that the main period of male attraction to light traps coincides with the "disappearance" from the breeding marshes emphasized by the Nielsens and interpreted by them as the period of dispersal. During this same dispersal period, Aug. 20–22 in this experiment, the females reached a distance of 20 miles, —although their light reactions did not permit them to enter traps in force until after the males no longer did so. Why then were not many more males caught at distant traps on Aug. 20–22?

If the males did not disperse beyond two miles, there should have been many more trapped within this distance. If the sex-ratio at release was 50–50, considerations of mortality and area would have resulted in a far greater density of males within one mile of the release point on Aug. 20–22 than of females within twenty miles on Aug. 22–25. Yet the per-trap, per-night captures of the latter (1.33) actually exceeded the former (1.20). Two possible explanations of this phenomenon may be considered. (1) The males accompany the females in their full migratory dispersion but since females are not attracted to light at this age, the males are likewise kept away from the orbits of light trap attractions; the male recaptures of this experiment would then represent non-migrants. (2) The males accompany the females in the initial exodus a short distance only and then fall out of migration; the small number of male captures within their small dispersion area would then indicate a lesser attraction to traps than that of females. The demonstration above of a lesser attraction to light traps for males of this brood makes the latter, favored explanation possible, but it does not disqualify the former.

SUMMARY

1. Radioactive *Aedes taeniorhynchus* adults were produced by exposing the larvae to radiophosphorus (P^{32}). The subsequent dispersion from Sanibel Island, Florida, was studied from the time and space distribution of marked recaptures. Other collecting methods were used but only light traps yielded significant numbers of recoveries.

2. Migration, as a special non-purposive flight, occurs from 1 to 4 days after emergence. This initial exodus carried females to the limits of the collecting area, 20 miles, and probably beyond. The males probably did not migrate beyond 2 miles. This main flight was deflected to the northwestward, possibly by prevailing southeasterly winds and by the NW-SE alignment of the coastline and topography.

3. Light traps collected females on a 5-day cycle of numbers; the last one was caught 19 days after emergence. Males entered light traps the first three days only after emergence; this has no bearing on their longevity.

4. There is some indication that females may migrate early in each 5-day progenitive period.

5. Dispersion of female *Aedes taeniorhynchus* appears to be a random, omnidirectional, appetential dispersal periodically repeated from foci established by a previous migratory, channeled, non-appetential dispersal. Males accompany the females on the initial exodus but probably drop out of the migration within a mile or two and thereafter settle down to a sedentary life characterized by swarming during twilight periods for 2–3 weeks.

ACKNOWLEDGMENTS

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