FIELD SURVIVAL AND OVIPOSITIONAL CHARACTERISTICS OF *AEDES AEGYPTI* AND THEIR RELATION TO POPULATION DYNAMICS AND CONTROL

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ABSTRACT. Approximately 34,000 adult *Aedes aegypti* (L.) were released on Seahorse Key, an island off the Gulf coast of Florida. Ovitraps were used to collect eggs over a 21-day period after the release to determine oviposition cycles, and adult females were caught to assess the number of eggs in a single oviposition. Oviposition began 5 days after release, and peaks occurred at 4-day intervals. The average number of eggs for a single oviposition was 93±6. A mean daily adult survival rate of 0.82 was calculated by linear regression of egg density on time (days) after release. Larval survival was strongly density-dependent in tests conducted in cages under ambient conditions. The adult survival and fecundity data were used to calculate rates of immature survival corresponding to assumed rates of population growth.

Our interest in genetic methods for controlling *Aedes aegypti* (L.) has led to experimental evaluations of the competitiveness of genetically-altered males in limited field tests (Seawright et al., 1975, 1976). During the course of these tests we obtained information concerning ovipositional cycles and fecundity of adult females. We also studied the survival of larvae at various densities. These data are presented here to give a partial view of the dynamics of *A. aegypti* in north Florida and to indicate the relevance of genetic control methodology to this species under these climatic conditions.

METHODS AND MATERIALS

ADULT STUDY. All larval rearing for the adult releases was done in an outdoor cage using water from a subterranean well. Groups of 1400 first stage

larvae were set in trays containing 6 liters of water infused initially with liver powder (0.93 g) and brewer's yeast (0.47 g); 4 days later 2.8 g of ground hog supplement were added. Most of the larvae pupated within 6–8 days, and sexual separation was accomplished with a pupal separator with 99% efficiency. Young adults were transported in cages by automobile and boat to one of the release sites on the island of Seahorse Key, which is located in the Gulf of Mexico about 2 mi. west of Cedar Key, Florida. The release area was as described in previous papers (Lowe et al. 1973, Seawright et al. 1975). The island is a rookery of the white ibis, and other wildlife typical of northern Florida are present, but our release occurred after the ibis had departed. We were thus concerned about the availability of blood meals for the female mosquitoes so 2 rabbits were caged in the center of the release area. On August 25, 1973, 18,000 translocation and normal males and 16,000 normal females were released on the island when they were 1-day-old virgin adults.

Oviposition was monitored by collecting all the eggs present each day in 20 buckets (lined with filter paper) and in eleven 55-gal barrels (lined with white cloth) distributed throughout the experimental plot and returning them to the laboratory where they were counted. Both types of containers were about half filled with water; the barrels were also being used in a concurrent study on *Culex pipiens quinquefasciatus* Say.

The second release site was a simulated breeding area just north of Gainesville in an isolated area of a pine-cypress forest, described in a previous paper (Seawright et al. 1975). During this experiment, oviposition was monitored by counting all the eggs collected in 3 buckets lined with filter paper. This release, on June 7, 1974, consisted of 3000 males and 3000 females of the same strain released on Seahorse Key. However, this strain had been maintained for 6 generations in the laboratory so some behavioral differences were expected.

LARVAL STUDY. During the summer of 1972, a population of *A. aegypti* was found breeding in a junk yard of discarded washing machines in Gainesville, Florida. Testing at that time showed 67% survival of 400 larvae reared in 10 liters of water drained from the machines (Wijeyaratne et al. 1974). We intended to follow this work with a more intensive study on larval survival in relation to density dependence during 1973. Unfortunately the owner began removal of the junked machines during April 1973 and by May, the lot was nearly empty. Because of this we drained 5 of the remaining machines and took the water to a site behind our laboratory. There we combined 1 liter of this water with 6 liters of water from a subterranean well and 2 g of leaf debris in a 3-gal bucket. Twelve plastic buckets prepared in this manner were covered with plastic screen and a piece of plywood to simulate a washing machine and allowed 3 wk to age prior to the introduction of larvae. Each bucket was assigned at random and seeded with 100, 500, 750, or 1000 1st stage larvae of the strain originally collected at the junkyard. Maximum and minimum temperatures of the water in the buckets and the number of pupae were recorded each day. Adults were scored for sex. The duration of this experiment was 60 days beginning on June 1.

RESULTS AND DISCUSSION

ADULT STUDY. Surveys of both release sites prior to the adult releases detected no indigenous *Ae. aegypti* at either site. Presumably the eggs collected during this experiment were due solely to the released females. Graphic summaries of the daily egg collections

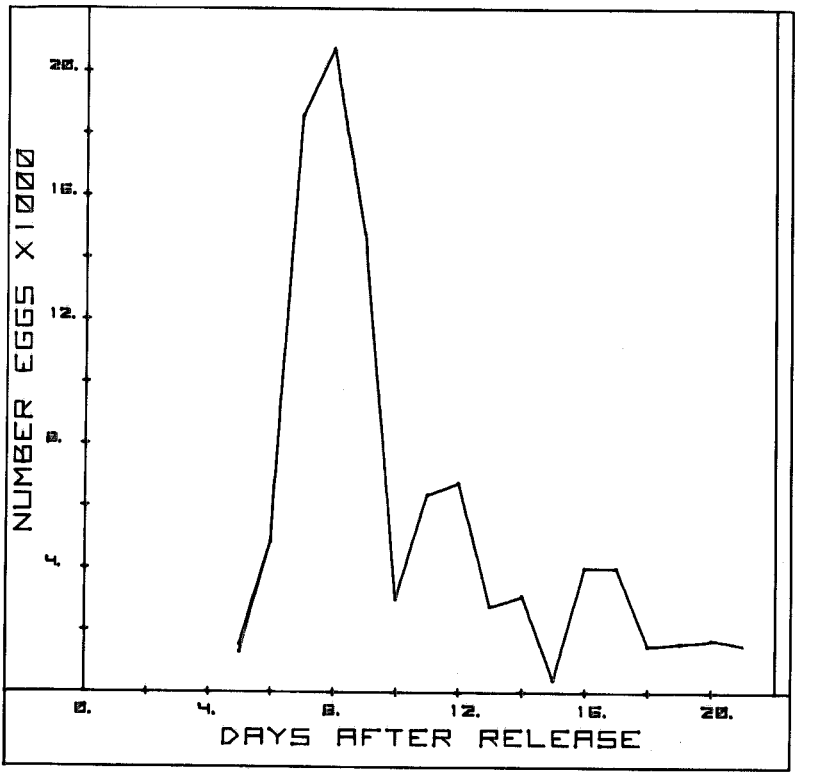

Fig. 1. Daily egg collections after the release of *Aedes aegypti* on Seahorse Key.

for Seahorse Key are shown in Figure 1. After both releases the first eggs were obtained when the adult females were 5 days old, and the subsequent pattern of oviposition appeared to follow a 4-day cycle with maxima on days 8, 12, and 16. This corresponded well with the 4-day gonotrophic cycle noted by Wijeyaratne et al. (1974) for *Ae. aegypti* in outdoor cages. A total of 96,652 eggs was collected on the island over a 22-day period. By grouping the eggs in 4-day cycles, we obtained totals of 63,192, 18,958, 8,275, and 5,700 for the 1st, 2nd, 3rd, and 4th oviposition cycles, respectively. The average number of eggs deposited in the laboratory by 44 females collected on the island was 93 ± 6 ($\bar{X}\pm S_{\bar{x}}$) for a single oviposition.

At the other site, a total of 61,954 eggs was collected over a 16-day period, and by grouping the eggs in 4-day cycles, we obtained totals of 40,384, 15,700, and 5,870 for the 1st, 2nd, and 3rd oviposition cycles, respectively. The average number of eggs of 124 females collected during subsequent mating competitiveness tests at this location was 95.9 ± 2.59. This compares very favorably with the value of 93.0 for females captured during the test on Seahorse Key.

Using the oviposition data, an estimate was made of the survival rate for the adult females. To do this, we made the following assumptions: (1) the number of eggs laid in successive ovipositions is directly related to the number of surviving females; (2) daily

mortality of adults is constant and (3) each successive oviposition produces approximately the same number of eggs. With these assumptions we then determined the mean adult survival rate (X) with the equation, $N_d = N_o(X)^d$, where:

N_d = number females alive on day d
N_o = initial number of females
d = day after release

By using logarithms the above equation becomes:

$\log N_d = \log N_o + \log X(d)$

which is the form of a linear regression with a y-axis intercept at $\log N_o$ and a slope of $\log X$. The egg totals for oviposition maxima were subjected to the linear regression analysis and a good fit (Figure 2) was obtained with a correlation coefficient (r^2) of 0.97 and a slope (=adult survival rate) of 0.82 for the Seahorse Key data. The upper and lower confidence limits of the slope were 0.87 and 0.77, respectively.

The calculations for the second site yielded a similar fit with $r^2 = 0.99$ and a slope of 0.785 (also on Figure 2). Upper and lower confidence limits around the slope were 0.790 and 0.781, respectively. These high correlation coefficients indicate that good estimates of the slopes were obtained, but the results of the analysis exposed an anomaly in our results on Seahorse Key. Extrapolating to the y-axis intercept, a value of 258,000 eggs was obtained. When we divided the intercept value by the average number of eggs per ovipositing female, we should have obtained a value

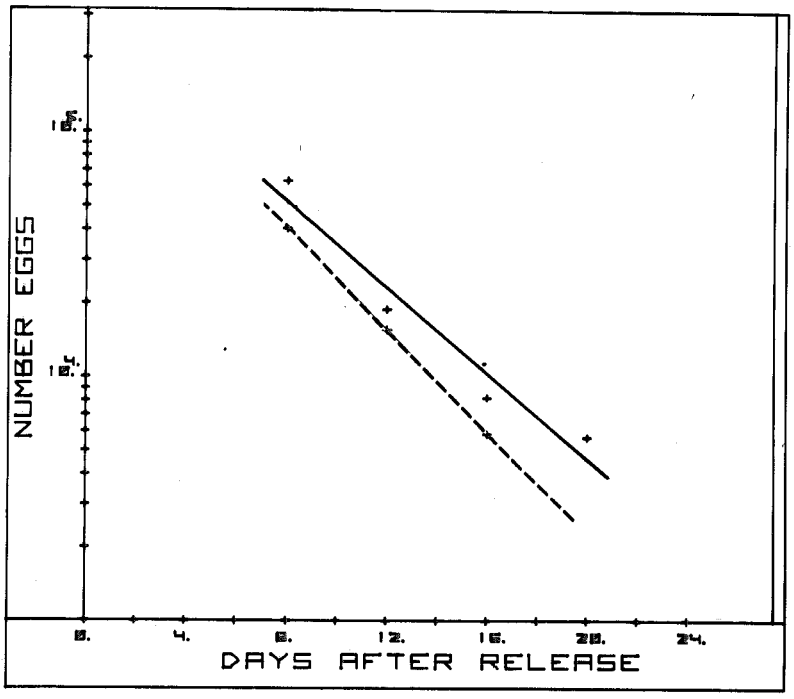

Fig. 2. Regression lines for 4-day oviposition cycle of *Aedes aegypti* on Seahorse Key (solid line) and Gainesville site (slashed line).

close to the number of females released on the island. Instead, 258,000 divided by 93 yielded 2770, only 17% of the 16,000 released females.

In contrast, when similar calculations were done for the second release, an estimate of 2940 females was obtained which was very close to the 3000 that were released. These observations could be interpreted to mean that in the second test we were sampling nearly the entire release population. In subsequent competitive mating tests at this same site we observed that the mosquitoes stayed in the general vicinity better than at several other experimental sites.

Because of the irregularity noted for the Seahorse Key data, we did the same type of linear regression analysis on data published by Lowe et al. (1973), wherein they described the oviposition cycles for *C. p. quinquefasciatus* Say on Seahorse Key. The regression line is shown in Figure 3 with a slope of 0.85 and a correlation coefficient of 0.99. The upper and lower confidence limits (0.95) for the slope (=survival rate) were 0.87 and 0.82, respectively. Extrapolation of the regression line to the intercept disclosed the same irregularity observed in the analysis of the *A. aegypti* data. They released 50,000 females, but the calculated intercept

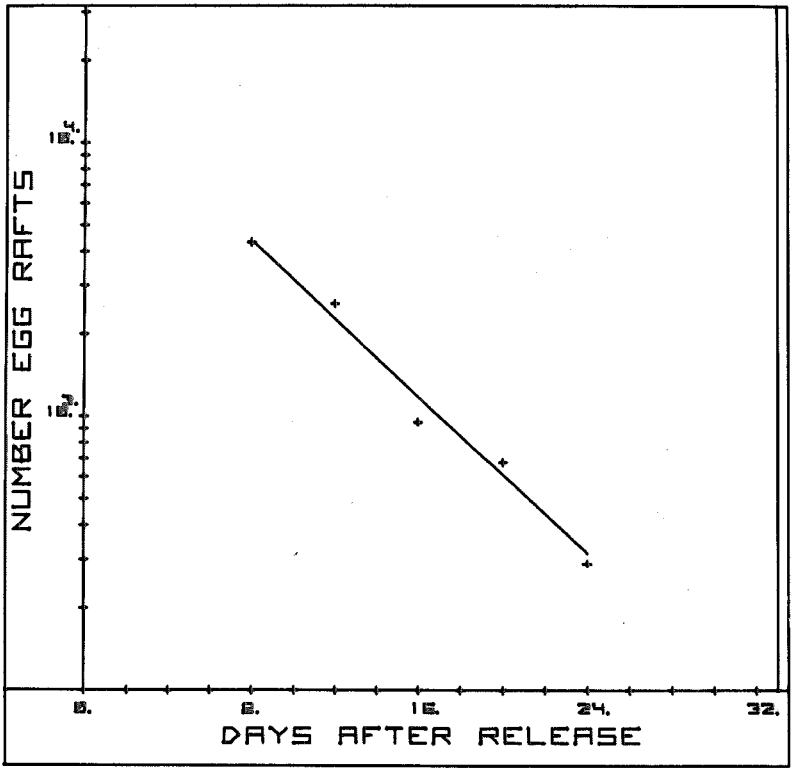

Fig. 3. Regression line for 4-day oviposition cycle of *Culex pipiens quinquefasciatus* females on Seashorse Key. The calculations were made on data published by Lowe et al. (1973).

value was only 13,642 (25%). Therefore, it seems reasonable to conclude that in both experiments the actual number of female mosquitoes sampled via oviposition was less than originally expected.

There are several possible explanations of this difference, e.g.: (1) a differential rate of survival whereby a constant rate of mortality does not occur but rather an initial low daily survival rate precedes a subsequent higher rate; (2) a density-dependent factor (or factors) that prevents adult females from ovipositing; (3) emigration from the central part of Seahorse Key and thus away from the oviposition sites; or (4) alternate indigenous oviposition sites that were not known and thus not monitored. Of the above possibilities, the latter two seem to be more plausible and certainly fit our observations and assumptions. If a density dependent factor did affect oviposition, it was apparently influential for not more than 4–6 days at the onset of the test, and did not affect survival estimates thereafter. Finally, if survival rates do in fact change with age, then our basic assumption is faulty and our observations may not measure what we think they measure. However, released insects must adapt rapidly to a new environment so after an initial period of abnormal stress and a low rate of survival, one might expect the survivors to exhibit a more favorable pattern of survival such as that calculated from data collected on days 5 through 22 with *Ae. aegypti*. Presumably such phenomena are not characteristic of indigenous populations.

LARVAL STUDY. The data collected in the larval survival experiment are summarized in Table 1 and Figure 4. The mean maximum and minimum temperatures were 84.7±3.3°F and 74.7±1.8°F, respectively, which provided fairly stable temperature conditions in the buckets throughout the experiment.

Larval growth was extremely slow and pupation extended over a 44-day period (Table 1). However, the mean development time (43 to 49 days) was similar regardless of the initial density of larvae, and even when the test was terminated, there were still a few larvae present in some of the buckets. In previous work (Wijeyaratne et al. 1974) a mean development time of 24 days was observed for 400 larvae reared in 10 liters of water from the same junkyard. It is likely that the slower growth rate was associated with the dilution of the water from the machines with well water. One might expect to observe a distinctly longer development time as larval density increases instead of the situation we observed (Table 1). Perhaps an insufficiency of nutrients in the water obscured any effect that density might exert on speed of development. Certainly density dependent factors were operative and limited larval survival, which dropped from 17.7% with 100 larvae to 1.3% with 1000 larvae. The sex ratio among adults produced was normal at all densities. The data we collected represent only the situation we created, and therefore, cannot be used to extrapolate to other rearing sites or to a situation in which larvae of various ages are present in the same container.

POPULATION DYNAMICS. Insight into the effectiveness of a control strategy can be gained by using biologi-

Table 1. Survival of larval *Ae. aegypti* reared outdoors (mean of 3 replications).

Initial larval density	Number of pupae	Percent pupation	Larvae remaining	Mean development time (days)
100	17.7	17.7	1.3	45
500	21.3	4.3	0.3	43
750	20.7	2.8	12.0	49
1000	13.0	1.3	13.0	46

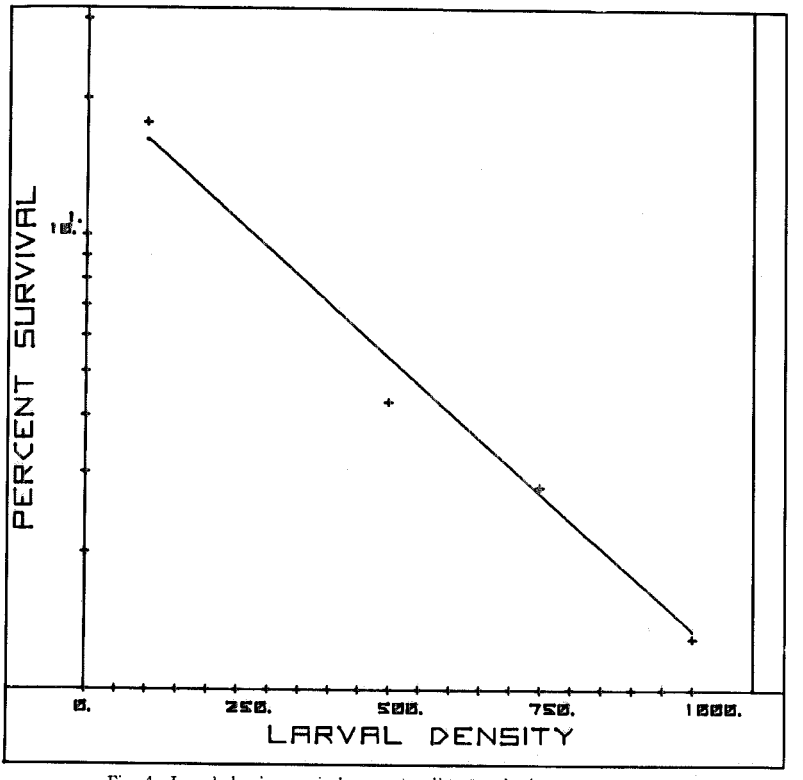

Fig. 4. Larval density survival regression line for the immature stages of *Aedes aegypti* reared in buckets.

cal parameters, e.g., fecundity, survival rates, and oviposition cycles, to calculate the potential growth rate of a mosquito population. Likewise, one can use assumed or measured growth rates to estimate other biological parameters (Weidhaas et al. 1974) by using the formula:

$$RI = bnSi--2$$

This formula simply states that the rate of increase from one generation to the next is equal to the mean number of egg batches per female (b) times the number of eggs per egg batch (n) times the rate of immature survival (Si) divided by 2 (since half of the progeny are males).

The observed daily survival of adults (0.82) and the average fecundity (93 eggs/female) from the Seahorse Key experiment were used to calculate rates of immature survival that would be necessary to obtain various rates of increase for *Ae. aegypti*. (This was done to relate the control potential of genetic control methods to the density-dependence of immature survival.) Generalizations can be made from the calculations shown in Table 2. For example, for a 10X rate of growth, the immature survival would be approximately the same as that reported by Wijeyaratne et al. (1974), which implies that *Ae. aegypti* populations in the junkyard dump had the potential to expand at a 10X rate of growth. If the rate of

Table 2. Rates of immature survival calculated from the estimated adult survival and observed fecundity data to correspond to assumed rates of population growth.

Rate of increase	Rates of immature survival corresponding to rates or adult survival		
	0.77 (lower limit)	0.82	0.87 (upper limit)
1X	0.12	0.06	0.03
2X	.24	.12	.06
3X	.35	.18	.08
4X	.47	.24	.11
5X	.59	.30	.14
6X	.71	.36	.17
7X	.83	.42	.20
8X	.95	.48	.22
9X	1.06[a]	.54	.25
10X	1.18[a]	.60	.28

[a] This value is purely theoretical since survival cannot exceed 1.0.

survival of adults was greater, then a growth rate greater than 10X would be possible.

We must emphasize that the data presented here, and also those of Wijeyaratne et al. (1974), were collected during the summer when optimum conditions in terms of temperature and rainfall exist for the expansion of a population of *Ae. aegypti*. We have found that this species does not occur in large numbers in north Florida except during the time interval from late May through early October. Unfavorable weather conditions probably limit *Ae. aegypti* during the rest of the year. Also, during the *Ae. aegypti* eradication program of the 1960's, density of field populations was assessed with ovitraps, and Jakob and Bevier (1969) summarized data collected in several sites in the southeastern United States. They reported for Orlando, Florida that ovitraps containing eggs of *Ae. aegypti* increased from nearly zero in mid April to about 50% in July. Similar data were collected in Waycross, Georgia, where 60–70% positive ovitraps were recorded for July. These data indicate a measurable rate of population growth during the spring and early summer for *Ae. aegypti*. The rather long duration for the immature stages would limit population growth and prevent a large buildup early in the summer.

Any genetic control effort with this species should begin before the summer buildup starts so as to diminish potential population gains, and because of the intensity of density-dependence factors during the larval stage, sterile males (with individual genetic loads of 100%) would represent the most efficient genetic control method. Reciprocal translocations or other such mechanisms would not be as appropriate, especially if eradication or rapid population suppression is desired because the genetic load possible with presently available genetic mechanisms (50 to 80%) would fall short of the biotic potential of this insect. To obtain population reduction at a time when the natural rate of increase is 10X, it is necessary to introduce genetic load in the indigenous population in excess of 90%. However, if one accepts the premise that reduction of a population below its full potential would lead to a smaller and more manageable population in the succeeding breeding season, then genetic mechanisms such as translocations would offer a useful tool and a promising method as is shown in Table 3. Although this is a simplistic model that avoids issues of fitness, competi-

Table 3. Theoretical calculations of populations that would be observed with varying genetic load and a rate of increase of 10X per generation.

Generation	Population size		
	No load	50% load	80% load
0	1	1	1
1	10	5	2
2	100	25	4
3	1,000	125	8
4	10,000	625	16
5	100,000	3125	32

tiveness, release ratio, etc., the point to be stressed is that any genetic load should cause some loss in population in the long run and will be detrimental simply because it prevents the full population potential. Field experiments are needed to determine the advisability of using genetically altered males for the control of *Ae. aegypti*.

Literature Cited

Jakob, W. L. and G. A. Bevier. 1969. Application of ovitraps in the U.S. *Aedes aegypti* eradication program. Mosquito News 29:55–62.

Lowe, R. E., H. R. Ford, B. J. Smittle and D. E. Weidhaas. 1973. Reproductive behavior of *Culex pipiens quinquefasciatus* Say released into a natural population. Mosquito News 33:221–227.

Seawright, J. A., P. E. Kaiser, D. A. Dame and N. L. Willis. 1975. Field competitiveness of males of *Aedes aegypti* (L.) heterozygous for a translocation. Mosquito News 35:30–33.

Seawright, J. A., P. E. Kaiser, N. L. Willis and D. A. Dame. 1976. Field competitiveness of double translocation heterozygote males of *Aedes aegypti* (L.). J. Med. Entomol. 13(2):208–211.

Weidhaas, D. E., S. G. Breeland, C. S. Lofgren, D. A. Dame and R. Kaiser. 1974. Release of chemosterilized males for the control of *Anopheles albimanus* in El Salvador. IV. Dynamics of the test population. Am. J. Trop. Med. Hyg. 23:298–308.

Wijeyaratne, P. M., J. A. Seawright and D. E. Weidhaas. 1974. Development and survival of a natural population of *Aedes aegypti*. Mosquito News 34:36–42.