increased by one or more blood meals. This was sometimes done by introducing a rat, enclosed in a screened tube, into a mosquito cage.

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BIONOMICS OF A POPULATION OF *CULEX PIPIENS QUINQUEFASCIATUS* SAY

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ABSTRACT. Calculations were made concerning the biotic increase (rate of successful reproduction) of an indigenous population of *Culex pipiens quinquefasciatus* Say exposed to the stress of total population control (release of chemosterilized males and the collection of egg rafts in ovitraps). Before control was applied, rates of increase from generation to generation varied from 1 to 3.5X, indication of a relatively stable population. Also, the rate of increase in the first generation after the stress was applied was the same as that in the generation just before stress was applied. Then, as control progressed toward suppression and eventual eradiction, the rate rose to 5.0X and finally to 10X (in about two to four generations depending on the environmental conditions). The normal rates of survival of the various stages in this environment probably limited the maximum biotic increase of this population to 10X.

The new integrated approaches to the control or suppression of insect populations in which sterility or genetic manipulation will play a part require quantitative information about the bionomics of populations as they exist in nature. Knipling (1968) stressed the importance of data relating to the total numbers of insects in a field population and their capacity to increase from generation to generation when he outlined the general requirements for suppression of insect populations through the introduction of sterility or by integrated techniques. Weidhaas (1968) proposed that such necessary bionomic information could be obtained by using sterility as a tag.

Recently, we reported two experiments in which sterile male mosquitoes, *Culex pipiens quinquefasciatus* Say (=*fatigans*), were released into an indigenous population on a small island, Seahorse Key, off the Gulf Coast of Florida (Patterson *et al.*, 1970a and b). The results of both tests demonstrated the validity of the concept of control of this mosquito by sterile-male releases; they also demonstrated the usefulness of induced sterility as a tag in obtaining bionomic data. Thus, we were able to calculate the absolute density of each generation of this specific population (expressed as the number of adults emerging into the population per unit time) and the percentage of the population of each generation remaining (after the application of the stress of total population control) to produce the next generation. In the present paper, we use these calculations to determine the actual biotic increase demonstrated in each generation of this population and explore the relationship between the mortalities of the various stages and the observed rates of biotic increase.

In the two experiments on Seahorse Key, the male *C. p. quinquefasciatus* used for the releases were reared at the laboratory in a carport and sterilized chemically (in 1968, by exposure of adults to tepa and in 1969, by exposure of pupae to thiotepa). In 1968, an average 2500 sterile males per day were released in August and September; in 1969, an average 13,300 sterile males per day were released in June, July, and August (range 8,400 to 18,000). In 1968, the population was reduced but not eliminated; in 1969, the population was essentially eliminated.

Seahorse Key is about 1 by 1/8 mile and is so situated off the Gulf Coast of Florida that it is 2 miles from Cedar Key and separated by 2 miles of salt water from the mainland and from other islands. Since larval breeding was confined largely to a septic tank and to assorted water-holding trash around buildings within a radius of 130 yards of the center of the island, ovitraps (12) could be located appropriately within this breeding area. The egg rafts were collected daily from these traps, and the number collected was used to measure the density of the population; also, the viability of the collected rafts was used to determine the effectiveness of the sterile males. Releases of males were all made at one point within the breeding area.

In 1968, while we were obtaining prerelease data concerning the population present on the island, the egg rafts were counted and returned to the environment; however, during the releases of sterile males, we destroyed the collected eggs after we had assayed them for viability. Thus, during the test, we were limiting the island population by (1) introducing sterile males and (2) by destroying egg rafts.

For our subsequent calculations, we first needed to know the percentage of the total egg rafts deposited on the island that were being collected and destroyed. We therefore used the figure of 50 percent established by Patterson and Smittle (unpublished data) when they tagged females on the island with ^{32}P to determine how many egg rafts were being collected from the ovitraps. If this 50 percent was accurate and relatively constant, we could use it to calculate the combined effect of the two stresses on the population. For example, suppose the total number of rafts deposited on the island was 100 during a given generation; then one-half (50) were destroyed by our collections. The remaining 50 (deposited elsewhere than in the ovitraps) would have the same percentage sterility (established by assay) as the collected rafts. If the collected rafts were 50 percent sterile, only 25 of the 100 egg rafts deposited would be viable, and the combined effect of the two stresses on the population would be a 75 percent reduction in reproduction, that is, in the number capable of reproducing.

In actual fact, in 1968, our assays showed 31 percent sterility among the average 144 egg rafts per day collected during the first generation, the first two weeks after the releases of sterile males began (Table 1). The 144 egg rafts per day that remained in the environment (same as number collected in ovitraps) were also 31 percent sterile. Then, since the 144 collected egg rafts were destroyed and 45 egg rafts were sterile, only 99 egg rafts per day of the 288 deposited were viable. The total percentage reduction of reproduction for that generation was then 65 percent (189 rafts destroyed or sterile ÷ 288 total rafts present). Table 1 summarizes these 1968 data.

Counts were made every day, but they were averaged for 2-week periods, the approximate time required for a generation to develop on this island (egg hatch = 2 days, larval development = 5 days, pupal development = 2 days, preoviposition time = 6–9 days). Those generations preceded by a minus sign in Table 1 are pretreatment (prerelease) generations. In June and July 1968, before the releases and removals were started, the population was increasing at relatively low rates, 1.4 to 3.5 times (X), an average of about 2.0X, indication of a relatively stable population in which each individual female was replaced in each subsequent generation by one to three females. (Large increases from generation to generation were not possible because of the relatively constant number of breeding sites for the immature stages.) Then from August through September as the sterile males continued to be introduced, sterility in the population rose to 85 percent, and the reduction in reproduction caused by the combined effect of the two stresses rose to 93 percent.

TABLE 1.—Results from the 1968 study of *C. p. quinquefasciatus*.

Month	Generation	Avg. no. egg rafts collected per day [a]	Percentage sterility	Percentage reduction of reproduction in a generation [b]	Percentage reduction in egg rafts [c]	Rate of biotic increase [d]
June	—3	20	0			1.5X
July	—2	30	0			3.5X
	—1	104	0			1.4X
Releases begun						
August	1	144	31	65	69	1.0X
	2	44	61	80	0	5.0X
September	3	48	75	88	0	10.0X
	4	58	85	93	21	10.0X
Releases ended						
October	5	46	51			

[a] About 50 percent of the total egg rafts oviposited each day were collected from ovitraps. These rafts were destroyed beginning with generation 1.

[b] Due to two stresses—sterility and removal of egg rafts; calculated from $\frac{A-AB}{2A}$ where A=no. egg rafts counted per day (=one half total no. eggs deposited per day) and B=percentage sterility of collected egg rafts.

[c] Reduction from one generation to next=$\frac{A_n-A_{n+1}}{A_n}$ where A_n=no. egg rafts collected per day in generation *n* and A_{n+1}=no. egg rafts collected per day in next generation.

[d] No. of egg rafts produced in generation *n*+1 divided by no. of egg rafts capable of reproduction in generation *n*.

The total percentage reduction in reproduction calculated for one generation compared with the actual population obtained in the next generation now allowed us to estimate the rate of biotic increase of this population. Specifically, the 65 percent fewer insects capable of reproduction in generation 1 as a result of releases and removal produced 69 percent fewer egg rafts for generation 2 compared with generation 1. Thus, the rate of biotic increase was 1.0X. Between generations 2 to 3 and 3 to 4, the actual numbers of egg rafts were not reduced even though the reductions in numbers capable of reproduction increased first to 80 and then to 88 percent. By calculation, these actual populations could not have produced these numbers of egg rafts unless the rates of biotic increase had been about 5.0X in generation 2 and 10.0X in generation 3. By generation 4, the last generation exposed to stress, the total reduction in numbers capable of reproducing had reached 93 percent, and the rate of biotic increase was 10.0X. Then between generations 4 and 5, it remained at 10.0X and the total percentage of reduction in density decreased another 21 percent. This unchanged rate of biotic increase compared with the increasing rates of earlier generations indicated that the maximum biotic increase (10.0X) for the population on the island at that time had been reached. The process then had required three generations, that is, about 6 weeks of stress. The experiment was discontinued because of adverse weather.

The 1969 experiment (Table 2) differed from the 1968 experiment in several respects though the overall results were similar. The second test was started earlier in the year, about the 1st of June, so we obtained little pretreatment data. However, those eggs collected in the last generation pretreatment (—1) were destroyed in 1969. In addition, when we started the releases of sterile males in 1969, the density of the population was about 2.8X higher than the density in 1968 (288 egg rafts per

TABLE 2.—Results from the 1969 study of *Culex pipiens quinquefasciatus*.

Month	Generation	Avg. no. egg rafts collected per day[a]	Percentage sterility	Total percentage reduction of reproduction in a generation[b]	Percentage reduction in density	Rate of biotic increase from 1 generation to the next
June	—1	228	0	50	36	1.25X
Releases begun						
	1	146	62	81	0	5.0X
July	2	151	85	93	69	5.0X
	3	47	82	91	80	2.5X
	4	9	84	91	10	10.0X
Releases ended						
August	5	8	95	98		

[a] Ovitraps collected about 50% of the total egg rafts oviposited each day. These rafts destroyed.
[b] Sterile and/or destroyed.

day in the —1 generation vs. 104). We also released larger numbers of males and obtained a greater percentage of sterility in 1969 (62 to 95 percent) than in 1968 (31 to 85 percent). Thus, when we added in the effect of destroying 50 percent of the egg rafts deposited, the final reduction in reproduction was higher in 1969 (81 to 98 percent) than in 1968 (65 to 93 percent). In 1969, the population was essentially zero by generation 5, no larvae could be found on the island, and there were very few viable eggs among the few egg rafts collected.

Specifically, in 1969, in generation —1, we destroyed about 50 percent of the egg rafts but did not release sterile males. The reduction in density from generation —1 to +1 was 36 percent, similar to that obtained in 1968 and the rate of biotic increase was about 1.0X. Then, since the percentage reduction in reproduction was 81 percent and there was no reduction in egg rafts between generations 1 and 2, the rate of biotic increase rose to 5.0X, also similar to the rise that occurred in 1968. Subsequently, in generations 2, 3, and 4, the total percentage reductions in reproductive capacity were 93, 91, and 91 percent, and the reductions in numbers of egg rafts deposited from generations 2 to 3 and 3 to 4 were 69 and 80 percent, respectively. Thus, the rates of biotic increase were only 5.0X and 2.5X between generations 2 to 3 and 3 to 4. Such large reductions in numbers of egg rafts occurring when the percentage reduction in reproduction was remaining steady at just above 90 percent indicated the presence of some control factor other than the releases of sterile males and the removal of egg rafts. In fact, excessive rain did occur during this period, and larvae were observed flooded and flushed from their breeding sites. Between generations 4 and 5, we again obtained a rate of biotic increase of 10.0X which we considered to represent the maximum possible for this population at this time (it was almost totally eliminated).

DISCUSSION. The similarity of the results obtained in the two experiments was of particular interest since it indicated that in this location, the maximum possible rate of biotic increase of this population was 10.0X. Moreover, in both years, when we started to impose stress on this population (essentially in balance because the rate of biotic increase was about 1.0X), it took three or more generations for the population to reach its maximum rate. In addition, in both tests, the downward trend in density began when the total percentage reduction in reproduction was above 50 percent; it could have been continued by maintaining the reduction above 90 percent.

Although we were concerned with the relationship between the mortalities of the stages of the species on the island and the rate of biotic increase, we did not make a special survey to determine how many of what stage were present. However, a rate of biotic increase of about 10.0X should be reflected in the patterns of survival of the egg, larval, and pupal (immature) stages and of the adult stage. Our observations at sites on the island where immature stages were developing before control began, that is, when the population was relatively stable, revealed that large numbers of eggs and first instar larvae were present and that only a few fourth instar larvae and pupae were present. Thus, when the population was stable, the rate of biotic increase was limited by the limited number of breeding sites for the immature stages. Then, when we reduced the number of viable eggs deposited in breeding sites by removing egg rafts or introducing sterile males, the proportion of those deposited that developed from the egg through the pupal stage probably increased or the time required for such development may have decreased because breeding sites and food became abundant. Either or both would account for the greater rates of biotic increase we actually observed, which approached the rate we obtain in our laboratory rearing (8 to 9 adults emerge from pupae developing from 10 eggs). However, 80 percent survival of immature stages would not result in the maximum rate of biotic increase observed in our field experiments. If one male and one female produce a total of 180 eggs (an average for single egg rafts on the island), the biotic potential (theoretical maximum rate of biotic increase) is 90X. Therefore, survival in the adult stage must also limit the rate of biotic increase and appears to be the most important limitation in a population such as this which is subjected to the stress of total control.

Patterson (unpublished data) showed that for every 100 females emerging each day into a population confined in a large field cage, only about 20 egg rafts per day were recovered; moreover, in a small isolated area where all the breeding sites were known, this figure was even lower (11 egg rafts per day for every 100 emerging females per day). Table 3 shows a pattern of female survival and oviposition if we assume an average rate of mortality of adult females of 25 percent per day

TABLE 3.—Hypothetical pattern of female survival and oviposition of 100 adult female *C. p. quinquefasciatus* and relationship to theoretical biotic potential of the unstressed population on Seahorse Key.

Day	No. of adult females surviving where average mortality is 25 percent per day	No. of females surviving to oviposit	Percentage of females in process of laying 1st, 2nd, 3rd egg rafts
1	100		
2	75		
3	56		
4	42		
5	32		
6	24		
7	18		
8	13		
9	10	10	93
10	8		
11	6		
12	4		
13	3	3	5
14	2		
15	2		
16	1		
17	1	1	2
18	1		
	Total = 398	Total = 14	

(slightly better survival than the best estimate obtained by Patterson). We do not know that this rate actually prevailed in our test, but we can use it to obtain an idea of the effect of reduced adult survival on egg production.

Unpublished data (Patterson) showed that the preoviposition time of the female *C. p. quinquefasciatus* in our study area to the deposition of the first batch of eggs was about 6 to 9 days; the majority of the rafts were deposited on days 8 and 9 and subsequent rafts appeared every 4 days. From Table 3, only 10 females would theoretically survive long enough to deposit a first raft of eggs; three would survive to deposit a second; and one would survive to deposit a third. Therefore, with our assumed rate of mortality of 25 percent of the females per day, we could theoretically expect 14 rafts from every 100 females emerging into the population. If the average egg raft contains 180 eggs, and 80 percent of the eggs survive through the pupal stage, then every 100 pairs would produce about 2000 progeny, a rate of biotic increase of 10.0X.

We do not know that the pattern of survival of females shown in Table 3 occurred on Seahorse Key. The table simply illustrates that relatively high rates of mortality among females would be necessary to limit the rate of biotic increase to the 10.0X that did occur. However, Patterson and Smittle, as noted, counted only 11 egg rafts on the island for every 100 emerging females. Therefore, the rate of mortality of females may well be relatively high in the study area during favorable breeding seasons.

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