Preliminary Observations on the Biotic Potential of ANOPHELES QUADRIMACULATUS

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The biotic potential concept implies the maximum rate of increase of an organism. In studying populations of a species some knowledge of its biotic potential is essential for proper interpretation of the fluctuations in the numbers of individuals. Furthermore, the severity of the environmental resistance (i.e. the pressure exerted by such environmental factors as temperature, wind, sunlight, abundance of predators, and limits of food supply and suitable resting places) exerted against the increase of a species becomes evident when the biotic potential and actual numbers of the species are determined. This is according to the simple relation expressed by Chapman (1928):

$$\frac{\text{Biotic Potential}}{\text{Environmental Resistance}} = \text{Actual Population.}$$

Thus, if we encounter two similar species about equally abundant in nature and find that one has two broods annually with 10 offspring per brood and there are equal numbers of each sex, while the other has one brood of 4 offspring each year and again the sexes are equal, we readily see that the environmental resistance against the former species is much greater than is the environmental resistance against the latter. Used thus, environmental resistance is the sum total of factors that militate against the increase of a given species, i.e. factors other than the species' sex ratio and the number of offspring produced.

Rogers, Hubbell, and Byers (1942) utilize as a convenient formula for expressing the biotic potential of a species: $PZ^n(R^{n-1})$, where P is the initial number of reproducing females, Z the number of offspring produced by each female, n the number of generations in the time interval chosen, and R the sex ratio (0.5 if the sexes are produced in equal numbers; 1.0 if the species is composed of parthenogenetic females). When the biotic potential of a form is calculated from this formula the figure obtained is the theoretical number of individuals that would constitute the last generation considered, and any survivors of intervening generations are not taken into account.

While biotic potential is an expression of a theoretical capacity of a species seldom if ever very nearly realized, it is of cardinal importance, as stated earlier, that it be determined for a species whose populations are to be studied. It is a fairly simple matter to supply values for most of the constants in the formula above as applied to the malaria mosquito, *Anopheles quadrimaculatus* Say, but the determination of a value for Z presents certain problems. The constant, Z,, represents the potential number of offspring each female would produce if all environmental influences were at optimum. One might assume genetic homogeneity in the species and take for Z the largest number of ova any individual female was ever known to deposit (assuming therefore that any failure by a female to deposit that complement of eggs was a reflection of some deterrent influence of the environment). On the other hand one might prefer, as a more appropriate figure for Z, the average number of ova per female determined from the individual egg laying experiences of a number of females. A female anopheline will take blood, develop a full complement of eggs and deposit them, take a second blood meal and develop and deposit a second complement of eggs, and in some instances repeat this process a number of times. This fact greatly complicates the determination of a value for Z in our formula, especially if we prefer an average figure.

Fortunately, we have available a colonized strain (the National Institutes of Health Q-1 strain) of *A. quadrimaculatus* whose individuals are so thoroughly domesticated that they may be manipulated in the laboratory with great facility. A brief description of certain insectary methods and some of the characteristics of this strain of *quadrimaculatus* should make more understandable the procedures followed in studying its biotic potential. An active colony of about two thousand adults (males and females) may be housed in a screened cage 2 x 3 x 3 feet. Mating occurs in the cage by the time the adults are a few days old, but it is necessary that the males be provided space to perform a mating swarm flight. The dimensions of the colony cage are adequate for mating of the colonized strain and as few as 100 males in a cage may perform an effective mating flight. Freshly emerged adults are quite soft, and few females will attempt to feed (take blood) until about 4 days after emergence. In practice, the female mosquitoes obtain blood from an immobilized rabbit placed in the cage for about an hour every day or several days each week. Every evening a pan of water is placed in the cage and the following morning it is removed with from five thousand to forty thousand ova floating at the water surface. Two or three days later the eggs hatch and the first instar larvae are fed pulverized dog chow sprinkled on the surface of the water. The larvae are distributed to several pans so that there will be no more than five hundred to one thousand per pan and are fed daily. About 3 weeks after oviposition the specimens will have passed through four larval stages and pupation then occurs. The papae are pipetted from the pans to bowls of water. The bowls are then covered by lantern chimneys closed at the top with netting. About 2 days later the adult mosquitoes emerge into the chimneys, and may be transferred to an empty cage to initiate a new subcolony or may be added to an existing colony to strengthen it. Virgin females reared in isolation take blood somewhat more reluctantly than fertile specimens and many refuse to feed; those that feed may develop and deposit a few infertile ova.

The procedures utilized for obtaining biotic potential data on the colonized strain were as follows: an empty cage was stocked with a large number of adults which had emerged in a 48-hour period. On about the 4th day the mosquitoes were permitted to feed on a rabbit. A number of females that had fed were removed from the cage within 2 days after feeding (at least 3 days are required for a female to develop and deposit ova after feeding). Each female was placed in a lantern chimney cage over a finger bowl containing tap water to a depth of 1 to 2 centimeters. Thereafter these specimens were examined daily by the insectary attendant* and were proffered a hand or arm at the open end of the chimney as a source of further blood, should the specimen desire to feed (see figure 1). When ova were present in a bowl they were counted and removed to the water surface in another appropriately labelled bowl.

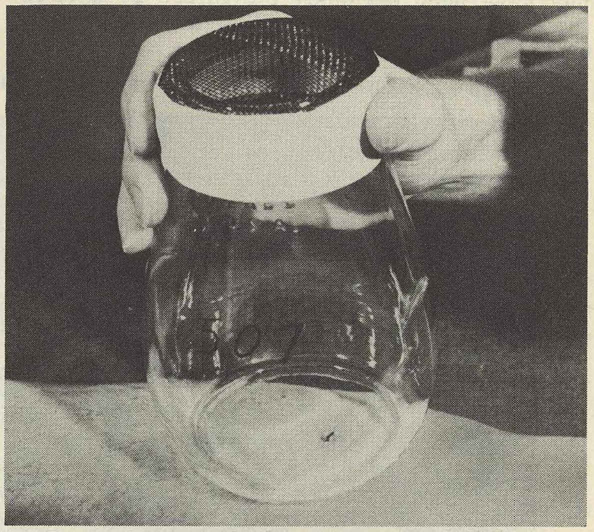

Figure 1. Feeding individual mosquito specimen on arm.

*Acknowledgement is made of the assistance of Biological Aide Robert P. Repass, who carried out by far the greater part of the operations described here.

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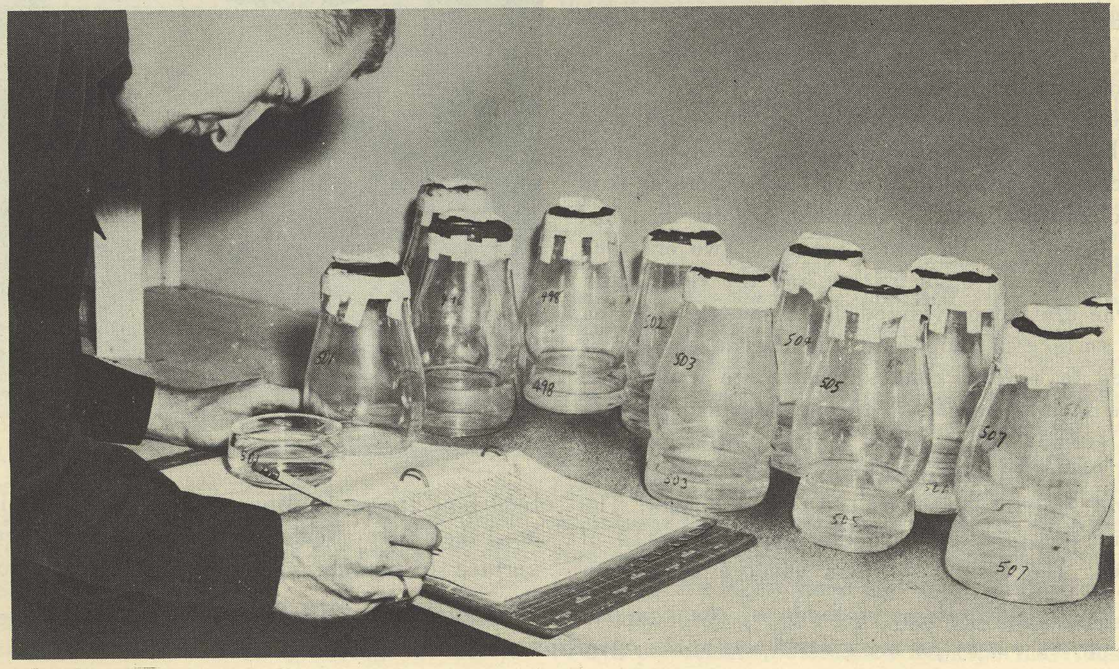
On subsequent days the bowls of ova were re-examined and 1st-instar larvae were removed, counted, and recorded as a check on the fertility of the ova. Thus separate records were kept on the number of ova and percentage fertility of successive batches of ova deposited by each female (see figure 2).

Twenty-six colony females were handled in this fashion. Thirteen followed a pattern of depositing ova of high fertility about every 3 to 5 days, taking blood after each oviposition. The total fertility of the ova from these females averaged 93.2 percent, and for the individual females, ranged from 85.3 percent to 97 percent. Of the other 13 females, 7 deposited no ova whatsoever and were probably infertile. Six others deposited few to many ova but in one way or another departed from the pattern of behavior exhibited by the 13 females mentioned above. The fertility of the ova of these six females was generally low, ranging from less than one percent to 79.2 percent. Since the 13 females which deposited ova of high fertility exhibited a similar pattern of behavior, it seems reasonable to assume that the activities of the other specimens may have been seriously prejudiced by environmental factors; i.e. these specimens may have been inadequately fertilized or may have been damaged in handling.

The 13 females of high fertility provided 13,090 ova, an average of 1,007 per female. The fertility of these ova was 93.2 percent. The group of 26 females considered as a unit provided 16,682 ova or an average of 641 per female; total fertility was 85.1 percent. Since 7 of these females did not oviposit, the 16,682 ova were obtained from 19 females, an average of 878 eggs per ovipositing female. Our "champion" female developed 10 distinct complements of ova, totalling 1,621, and deposited them in 14 batches (oviposition occurred on 14 different nights); 1,510 or better than 93 percent of these ova hatched.

We may now supply a value for Z in the biotic potential formula: 1,007, the average oviposition of 13 highly fertile females; 878, the average oviposition of the 19 egg-laying females; or 1,621, the greatest number of ova known to have been deposited by any single specimen. For practical purposes it may be assumed that the species, *A. quadrimaculatus*, is composed of equal numbers of males and females; therefore in

Figure 2. Examining lantern globe isolation cages and making oviposition records.



the formula R becomes 0.5. Actually our experience in the insectary and that reported elsewhere indicates that there are slightly more males than females.

Six is probably a conservative estimate of the average number of annual pedigree generations of *A. quadrimaculatus* in the southeastern coastal plain, although there would probably be broad overlapping between earlier and later generations. Boyd (1927) provided field data which he believed indicated 8 to 10 annual generations of this species in south Georgia and at least 7 in northeastern North Carolina, and Hurlbut (1943) calculated that there might be 9 or 10 annual generations in northern Alabama.

If we wish to accommodate the fertility factor, F, our original formula becomes:

$$P\ (FZ)^n(R^{n-1}).$$

By substituting in the formula the values derived above, the ultimate theoretical one-season progeny of EACH fertile female present in the spring may be calculated. The value for P will be 1 since the offspring from one beginning parent are to be calculated. The number of generations, n, will be 6; R will be 0.5; F will be 0.932; and Z, 1,007; the last two values being those provided by the 13 females of high fertility. Therefore:

$$1 \times (0.932 \times 1{,}007)^6\ (0.5^5) \text{ or}$$

21,356,115,775,836,710 individuals would constitute the theoretical sixth generation population that would be derived in a season from a single female. This calculation assumes, of course, that the environment for all individuals of each generation is optimal. Such a figure as that obtained is an obviously fantastic one and serves to show:

1. The strength of the total restraining influence (i.e. environmental resistance) against
2. The tremendous potential (actually explosive) capacity of the species to increase.

Although reports of fluctuations in actual field populations of *A. quadrimaculatus* indicate some extremely rapid rates of increase over short periods of time, no sustained rate of increase approaching the potential capacity of the species is ever reported.

It should be mentioned that the largest number of ova that we have been able to obtain from any single female *A. quadrimaculatus* collected in the wild is 575. We have isolated 150 adult females collected in the field at different seasons and have handled them in much the same manner as the procedure described for handling isolated specimens of the colony strain. Eighty-eight of these deposited no ova and many others deposited small and irregular batches. The laboratory conditions of confinement to which specimens being tested are subjected are indubitably less disturbing to specimens of the colonized strain than to specimens taken in the field. Also, the action of selective processes operating through many generations of the highly domesticated strain may have provided the colony insect, genetically, an entirely different biological (physiological) reaction system from that of the undomesticated population. Much in our insectary experience would indicate this.

It is interesting that wild-caught specimens of *Anopheles punctipennis* (Say) when isolated in the laboratory exhibit an egg-laying pattern that closely approximates that of the colonized strain of *A. quadrimaculatus*, while specimens of *Anopheles crucians* Weid. behave, in this respect, more like the wild specimens of *A. quadrimaculatus*.

References

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