MEASURING REPRODUCTIVE POTENTIAL IN POPULATIONS[1]

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INTRODUCTION. A possible strategy for controlling vectors of human disease agents is through the competitive displacement of the vector species by a non-vector species or strain (Knipling *et al.*, 1968). For example, Gilotra, *et al.* (1967), have suggested that naturally-occurring competitive exclusion has allowed *Aedes aegypti* (L.) to suppress *A. albopictus* (Skuse) populations in certain areas of southeast Asia. Gubler (1970) has examined several biological attributes of *Aedes albopictus,* a non-vector of filariasis, which allow it to outcompete *A. polynesiensis* Marks, the major vector of filariasis in the South Pacific. Following successful laboratory trials, Drs. Lloyd Rozeboom and Leon Rosen (personal communication) have recently released *A. albopictus* on a small island in French Polynesia in an attempt to suppress *A. polynesiensis.*

Both Gilotra *et al.* and Gubler were concerned with reproductive potential, or as they define it, the net reproductive rate of the competing populations. Their arguments were derived from a review by DeBach (1966) who suggested that if two ecological homologues are equivalent in their habitats and needs, then that population which produces the greatest number of female progeny per unit of time will replace its less productive competitor. This statement is true. However, DeBach argued further that a population need only have R_0 (net reproductive rate) greater than 1 to displace its competitor (which he implies has a R_0 of 1.). This is not necessarily true as will be shown below.

The purpose of this paper lies not with a critique of competitive exclusion and its demonstration; instead, I would like to show the use of R_0 to compare the reproductive capabilities of two populations. Attention is directed toward using the intrinsic rate of increase, r, as an alternative measure of competitive ability.

MATERIALS AND METHODS. Life tables were constructed from observations on the age-specific mortality and fecundity schedules of two laboratory strains of *A. aegypti,* TRIN and GKEP. The former strain originated in Trinidad in 1954 and the latter from Ghana in 1960. Additional information on these strains is given by Crovello and Hacker (in press).

For each strain, life tables were constructed from four replicate cohorts each consisting of 25 male and 25 female adults. The cohorts were established by allowing a group of around 200 females to feed on a chick 7 days after emergence. Twenty-five fully-engorged females were then placed in a cage with 25 males from the same egg batch. The cages were constructed from paper cylinders of 4 liter capacity, with nylon mesh covering the top of the cage. Access to the cage was through an opening cut in the side of the cylinder and covered with tubular stockinette. Cages were maintained in an environment kept at $27\pm2^\circ$ C, 80 percent r.h. and daylength of 16 hrs.

At 2-day intervals dead mosquitoes were removed and counted and a fresh oviposition cup was provided, a process that was continued until the last mosquito died. The number of eggs laid by the cohort during the time interval was counted and recorded. At 4-day intervals an anesthetized mouse was placed on each cage for 20 minutes.

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These life tables represent the controls from an experiment designed for a purpose other than that given here. This point is made to explain why the 7-day-old mosquitoes were used instead of freshly emerged ones, and why mice were used after an initial blood meal on a chick. Since the pattern of reproduction is the point of interest here, it is necessary only that the strains be treated in similar manner.

All data were recorded on punched cards and life tables were constructed using LIFE and LIFE 2, computer programs written by the author. The formulae programmed were standard life table entries such as described in Southwood (1966). A complete description and a listing of the programs are available from the author.

RESULTS. Although complete life tables were generated from the data collected, only certain summary statistics for the females are required for the present purpose. These are listed in Table 1, and include:

1. The life expectancy of the cohort at the first interval, i.e., the mean length of life.
2. The net reproductive rate (R_o), i.e., the mean number of female progeny produced by one female in her lifetime.
3. The intrinsic rate of increase (r), i.e., the number of females produced per female per unit of time in an unlimited environment.

DISCUSSION. From Table 1, it can be seen that the R_o of GKEP is about twice that of TRIN. Therefore, GKEP will produce twice as many progeny *per generation* as TRIN. On the other hand, the r's of the two strains do not differ significantly and a TRIN population will grow as rapidly as a GKEP population *per unit of time*.

The phrases, *per generation* and *per unit of time* have been italicized to emphasize the fundamental differences between these ways of expressing reproductive potential of a population. The differences can be appreciated when the formulae for R_o and r are examined below:

$$R_o = \Sigma l_x m_x$$

where l_x is the probability that a female will survive to age x,
and m_x is the mean number of progeny produced by a female of age x.

It can be seen that age, x, (i.e., time) does not enter this equation except for tabulating purposes (i.e., as subscripts). The only variables are the probability of surviving and the number of progeny. The actual length of a generation has no influence on the calculation of R_o. For example, it can be demonstrated quite simply that if two cohorts produced a mean of 10 females per female each during the life time of the cohort, then the R_o of both cohorts will be 10, even if

TABLE 1.—Summary life table parameters for two strains of *Aedes aegypti*. The values given are the means of four cohorts followed by the standard deviation in parentheses.

Strain	No. females tested	Mean generation length of females (in 2 day intervals)	Mean (and S.D.) reproductive potential: No. female progeny produced by one female in her lifetime (R_o)	Mean (and S.D.) reproductive potential: No. female progeny produced per female per unit of time (r)
TRIN	100	7.48 (1.25)[a]	56.3 (7.18)[a]	0.441 (0.021)[b]
GKEP	100	17.18 (4.19)[a]	125.6 (38.2)[a]	0.419 (0.032)[b]

[a] Difference significant $P<0.01$
[b] Difference not significant

the mean life of one cohort is 10 days and the other is 100 days.

For comparison, r is calculated from the relation:

$$1.0 = \Sigma l_x m_x e^{-rx}$$

where l_x and m_x are as defined as above and e is the base of the natural logarithm.

Note how age, x, is not only used for tabulating purposes, but also enters the equation as a variable. Therefore, not only the number of progeny produced, but also the ages during a cohort's history at which these progeny are produced, will have an influence on the intrinsic rate of increase. In the example above, the cohort with the longer generation time will have an r that is equal to or less than the r of the cohort with the shorter generation. The actual value of r will be determined by the ages at which reproduction occurred.

Now if Table 1 is again examined, the mean length of life for GKEP is 17.10 intervals compared to that of TRIN which is 7.46 intervals (an interval equals two days). Therefore, while GKEP females produce on the average twice as many progeny as TRIN females during their lifetime, the TRIN females produce their progeny in one-half the time. The result of these patterns of reproduction is that the R_0 of GKEP is twice that of TRIN, but the r's of the strains do not differ.

In application, the choice of R_0 or r to estimate the reproductive potential of a population will be influenced by the life history and mortality factors operating on the population under study. For univoltine species, the R_0 may be sufficient to compare the reproductive potentials of the population. However, with multivoltine species, especially those with overlapping generations r would be preferable since it better reflects the growth potential of the population per unit of time. This may be particularly important when the outcome of competition is influenced by the species exploiting a resource first.

Returning to Gubler's paper (1970), he states that *A. albopictus* has a higher net reproductive potential (90.77) than *A. polynesiensis* (88.94) and would therefore have the advantage if the two species were competing in the same ecological niche. However, in this paper, he also gives a LT 50 (which appears to be the median length of life) of 67 days for *A. albopictus* and 47 days for *A. polynesiensis*. If the two species are producing progeny throughout their life time, then one would expect the r of *A. albopictus* to be less than that of *A. polynesiensis*. Since these species are multivoltine, and assuming that mortality factors operate proportionately on both, then *A. polynesiensis* would actually outproduce *A. albopictus* over the same interval of time, other things being equal. In point of fact, other things are not equal, and the outcome of competition between *A. albopictus* and *A. polynesiensis* is dependent more on the delay of larval development and on sterility due to cross-specific insemination (Gubler 1969). Given the probable higher intrinsic rate of increase of *A. polynesiensis,* then its elimination by *A. albopictus* through factors studied by Gubler (1969) is even more dramatic.

Finally, while the demonstration of the effect of pattern on the reproductive potential of a population could have been accomplished using mathematical analysis (e.g., see Lewontin, 1966; Cole, 1954), the presentation of experimental data on *A. aegypti* emphasizes the variability in reproductive pattern that occurs *within* a species. Since an ecological homologue that would competitively displace a vector species might best be found or constructed from a strain within the species, these data bring attention to the necessity of considering the reproductive patterns of competing populations.

SUMMARY. The intrinsic rate of increase and the net reproductive rate are compared as measures of the reproductive potential of a population. For multivoltine mosquito populations, it is proposed that the intrinsic rate of increase

may better express the reproductive potential of a population. A numerical illustration using two strains of *Aedes aegypti* is given.

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COLONIZATION OF *CULEX (MELANOCONION) AIKENII* (AIKEN AND ROWLAND, 1906) IN PANAMA [1]

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INTRODUCTION

Culex mosquitoes of the subgenus *Melanoconion* have been recently incriminated as vectors of arboviruses, pointing to the need of laboratory colonies of one or more species of this group of culicines for use in transmission experiments.

There have been three laboratory colonies of *Culex* (*Melanoconion*) mosquitoes reported in the literature. There was one colony of *C. portesi* at the Trinidad Regional Virus Laboratory (Takahashi, 1968), a second one of *C. cedecei* Stone and Hair, 1968 at the Communicable Disease Center (Hair, 1968), and a third of *C. peccator* Dyar and Knab, 1909 at Lake Charles, La. (Chapman and Barr, 1969). None of these colonies has reached a high enough population level to permit its use in experimental transmission work with arboviruses.

Culex (*Melanoconion*) *aikenii* came under suspicion as a potential vector of Venezuelan equine encephalitis (VEE) in the Middle Chagres river basin in the Panama Canal Zone, during studies conducted there by S. Srinhongse and P. Galindo of Gorgas Memorial Laboratory, Panama (unpublished). Recently, Galindo and Grayson (1971) successfully transmitted VEE to laboratory hamsters

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