

Selection for Colonizing Ability

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The problem of the optimal genetic and phenotypic characteristics of a colonizing species can be posed at three levels of differentiation. At the first, one may ask what the ideal colonizing species would be like and the answer is so easy to give that it is trivial. Obviously, effective dispersal, high somatic plasticity, and high interspecific competitive ability are all desirable and the greatest degree of all three is most desirable. But this reduces the problem of colonizing species to a trivial one. The best possible organism is easy to specify. At the second level we abandon the notion of the best possible organism and ask which among the existing genetic systems are more favorable for colonization. Will weeds tend to be selfers rather than open-pollinators, annuals rather than perennials, and so on? These broader questions are treated by Stebbins, Baker, Ehrendorfer, and others in this symposium. They are more pertinent in plants and in certain classes of lower invertebrates than in the higher animals where a diversity of genetic systems is not so evident, although the insects, as a whole, do have a diversity of genetic systems almost approaching that of plants.

It is the third level of variability that I would like to discuss, the variability ordinarily available within a species, variability of a more subtle kind whose selection does not involve a total remaking of the species. We must realize that the possibilities for selection in a population are not unlimited, that the genetic structure of a population is the result of a compromise among various selective exigencies so that it is not possible, in any short time, for natural selection to cause an increase in fitness with respect to every stage of the life cycles and every metabolic activity. An increase in fecundity may entail, in the absence of a complete remaking of the reproductive system, a reduction in viability or a longer development time. Thus, when we ask about the result of

natural selection in any immediate sense we must assume that only small increases in fitness can be made and that all aspects of the physiology and morphology cannot be remade drastically and independently. It is no use to point out that a *Drosophila* with a cerebrum, a vertebrate eye, and an opposable thumb would be an advantage over other *Drosophila*. That might be true, but it has nothing to do with natural selection.

In order to investigate the effects of selection for colonizing ability or selection in a colonizing species it is necessary to define colonization in a broad sense. Colonization is the establishment of a population of a species in a *geographical* or *ecological* space not occupied by that species. Rather than speaking of colonizing *species*, it is of more general interest to consider *colonizing episodes* for any species, that is, instances of colonization by some population of the species. Looked at in this way species lie in a continuum from ecologically and geographically restricted forms like the *Sequoia* to roadside weeds, from species with extremely rare colonizing episodes to those whose entire life pattern is one of colonization. For example *D. melanogaster* and *Anthonomus grandis* are rather far in the direction of colonizing species, since colonizing episodes occur every spring when the small overwintering population begins to increase in the absence of any population pressures.

This absence of population pressures is the mark of a colonizing episode and the population can be assumed to be growing exponentially with unlimited resources, at least for a short time. This does not mean that the population increases rapidly, but only that it is in the exponential growth phase and is essentially density independent.

For this reason that first part of this paper will be devoted to a consideration of the effects of selection in a population growing in an unlimited environment.

The second aspect of colonization, although not without exception, is the change in direction of selective forces that may accompany a colonizing episode. A newly formed colony is at first low in density and the individuals are in competition with individuals of *other* species, as opposed to the situation in older populations where any competition is primarily with members of the same species. In addition, the physical factors of the environment are likely to be rather different in a newly colonized area. For this reason the second part of this discussion will be concerned with the results of occasional radical alterations in selective forces on the genetic constitutions of the populations.

Finally, it is in the colonizing species that the possibilities are greatest for interdeme selection. Colonies are not always successful, perhaps usually not when they involve expansion of area and ecological tolerance. Thus many colonizing episodes must end in failure, and this means that

population characteristics can be selected as a whole by the frequent extinction of whole demes. In this way questions of *optimal* genetic characteristics become important since there is a mechanism for the selection of optimal strategies.

SELECTION OF LIFE CYCLE COMPONENTS

In an extremely interesting article in 1954 Cole discussed the effects of changing various aspects of the life cycle on the intrinsic rate of increase of a species. In particular he was concerned with major changes in life cycle phenomena such as the change to iteroparity. I should like in this paper to consider much smaller changes in life cycle phenomena such as small changes in fecundity, longevity, length of developmental period, etc., on the rate of increase. Such a study will reveal the relative selective advantages of genetic changes affecting these different life cycle phenomena. Underlying such a study is the assumption that selection cannot act on all the genes of an organism simultaneously in a major way because the available selection differential is limited and because of the physiological correlation among different aspects of the phenotype. Obviously, an animal with a higher fecundity, a greater longevity, a faster development will be at an advantage. But the real question, and thus the interesting one is "What is the relative advantage of increased fecundity of a certain amount as opposed to greater longevity?" The answer to such a question will give an insight into the direction in which populations will change during a colonizing episode.

Following our original assumption that during a colonizing episode the population is growing exponentially, the Volterra equation will hold and

$$\int_0^{\infty} e^{-rx} l(x) m(x) dx = 1 \quad (1)$$

where r is the intrinsic rate of increase of the population; $l(x)$ is the probability of an individual living to age x from age 0; $m(x)$ is the number of offspring produced per unit time at age x .

We now wish to ask how different changes in the age-specific mortality and fecundity schedules, $l(x)$ and $m(x)$, affect r . To do this we need a reasonably simple form of $l(x)m(x) = V(x)$, i.e., one that is integrable, and has a fairly realistic shape, yet which can be varied by the variation of relatively few, biologically meaningful parameters. A function which satisfies these criteria is a triangular V -function shown in Fig. 1.

$V(x)$ may be interpreted as the age specific fecundity schedule adjusted for the probability of survival to age x . A , T , and W are the age of first reproduction, peak reproduction ("turnover point"), and last

offspring, respectively. The total lifetime offspring production of an individual from birth is then given by the area under $V(x)$, that is by

$$S = \int_0^{\infty} V(x) dx = \frac{(W - A)}{2} V(T) \quad (2)$$

It will be possible with such a function to vary independently the total offspring production, S , and the pattern of reproduction in terms of the total length of life, age to first offspring, steepness of fecundity increase, and decrease with age, and so on. That this model is a reason-

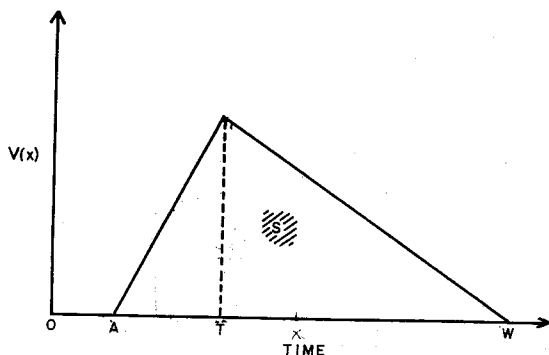


FIG. 1. Generalized triangular reproductive function, $V(x)$. A is age of first offspring; T , turnover point; W , age of last offspring; S , total number of offspring.

able approach to real $V(x)$ curves is shown by Figs. 2-4 which show schedules for *Calandra oryzae* (Birch, 1948) and *D. serrata* (Birch *et al.* 1963). It is only the general shape we are concerned with and not the finer details of departures from linearity.

Some elementary algebra and geometry applied to Fig. 1 gives the following relationship

$$\begin{aligned} V(x) &= \frac{2S(W - x)}{(W - T)(W - A)} & x \geq T \\ V(x) &= \frac{2S(x - A)}{(T - A)(W - A)} & x < T \end{aligned} \quad (3)$$

Substituting Eq. (3) in Eq. (1) gives the expression relating the rate of increase r to the parameters S , A , T , and W .

$$\frac{(W - A)r^2}{2S} = \frac{1}{T - A} [e^{-rA} - e^{-rT}] + \frac{1}{W - T} [e^{-rW} - e^{-rT}] \quad (4)$$

This implicit expression can then be solved numerically for r under various conditions.

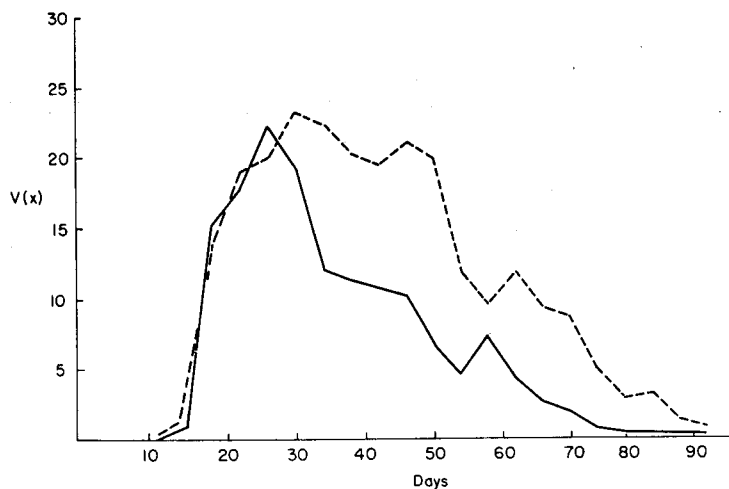


FIG. 2. Observed $V(x)$ -functions for two races of *D. serrata* at 25°C. Both $V(x)$ -functions give the same value of r because of lack of contribution of later ages to the rate of increase.

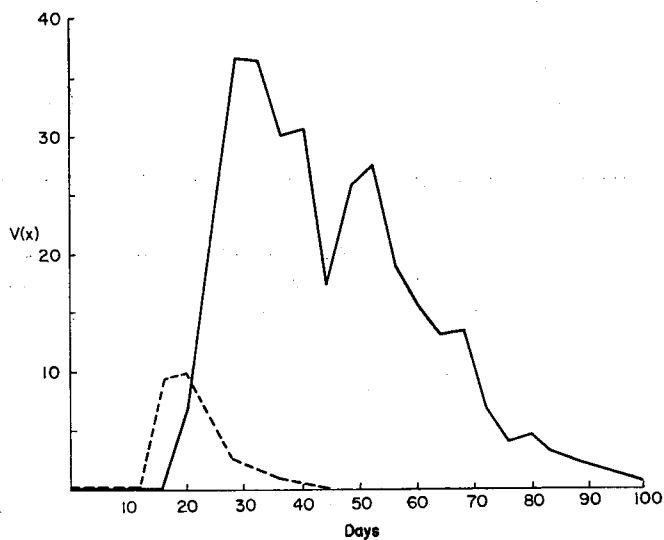


FIG. 3. Observed $V(x)$ -functions for two races of *D. serrata* one at 20°C (solid line) and one at 25°C (dashed line). Both $V(x)$ -functions give the same value of r because of the overriding importance of leftward displacement of the dashed curve. Difference in total offspring is a factor of 10.

The results of such solutions are shown in Figs. 5-8. In each case the abscissa represents total productivity S on a logarithmic scale. On the ordinate for each graph is one of the parameters A , W , or T . The lines connect points of equal r so that each graph is really a response surface showing how r decreases or increases with joint changes in S and one of the other parameters. With the help of such response surfaces it is possible to answer the following sort of questions. In order to increase r from 0.270 to 0.300 how much does fecundity have to be increased for

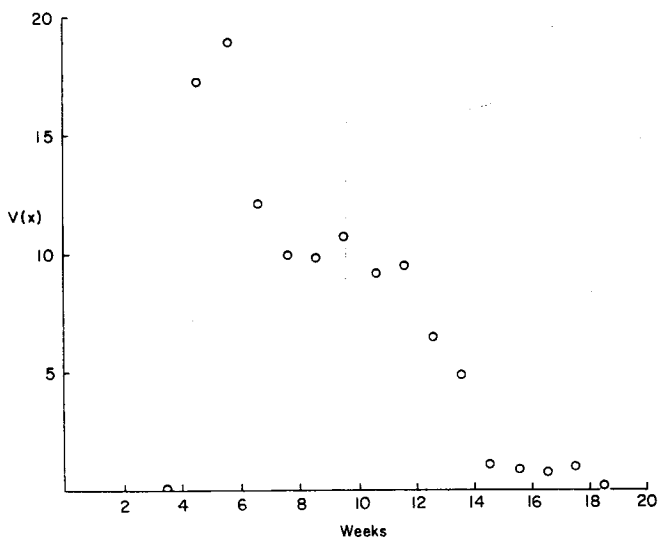


FIG. 4. Observed $V(x)$ of a beetle *Calandra oryzae* at 29°C. From Birch (1948).

different developmental rates? A decrease of how many days in time to first egg is equivalent to a doubling of fecundity? The figures are arranged in decreasing order of the effect of the time parameter variation. In Fig. 5 we see the effect of simply shifting the whole $V(x)$ schedule earlier and later without changing its shape. The dotted line represents a base configuration corresponding to $A = 12$, $T = 23$, $W = 55$ for comparison with other graphs.

We see, for example, from the upper right section that a doubling of total fecundity from 5000 to 10,000 offspring can increase the r from 0.510 to 0.565 but that an equal increase would come from reducing development time (time to first egg) from 8.6 to 7.5 days. Thus one day saved in development is worth a doubling of fecundity or 5000 eggs. At the opposite end of the scale where fecundity is low a doubling of

fecundity from 150 to 300 eggs will increase r from 0.180 to 0.205 and this is equivalent to a 3-day shortening of development from 16.2 to 13.2 days.

Figure 6 shows the effect of varying the date of the first egg, while holding other times constant. This changes the shape of the fecundity

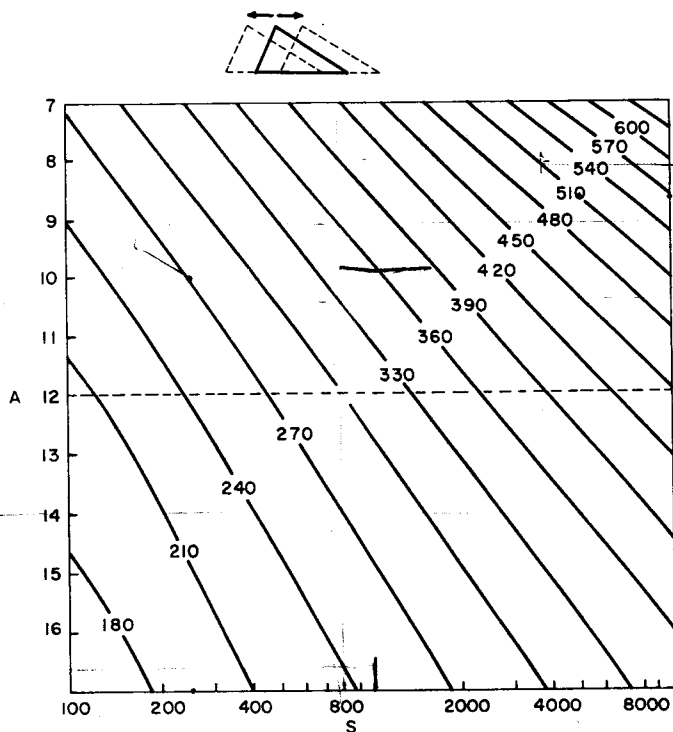


FIG. 5. Response surface showing equal r lines for different total offspring numbers and different locations of the $V(x)$ -function along the X axis. The dashed line corresponds to $A = 12$, $T = 23$, $W = 55$. Changes in A shown on the ordinate also have equal accompanying changes in T and W .

curve causing steeper or shallower rate of increase of fecundity. Figure 7 shows the effect of varying turnover time, while holding A and W constant. The changes in shape of the V -function here are concerned with the proportion of eggs laid before and after the turnover point. Finally, Fig. 8 shows the effect of extending the period of egg laying (changing W) without increasing total fecundity. As might be expected such extension actually lowers r because eggs have been postponed but not increased.

To compare these four curves we can use as a reference point the intersection of the $r = 0.300$ contour with the base reference line. The change in the number of eggs necessary to increase r from 0.300 to 0.330 is the same in all cases, of course (780 eggs to 1350, nearly a doubling).

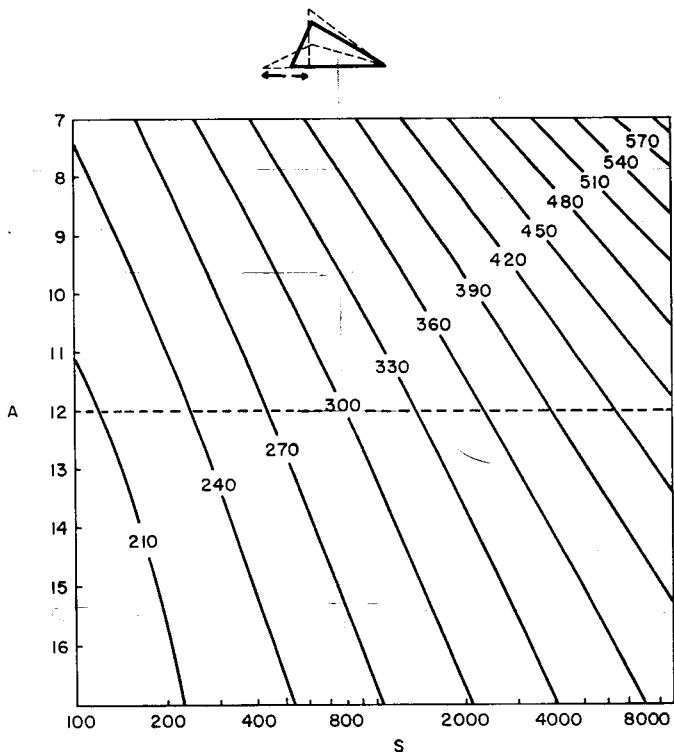


FIG. 6. Response surface showing equal r lines for different total offspring numbers and different A values with $T = 23$ and $W = 55$.

The number of days needed to be equivalent to this increase in fecundity for the four cases are:

- | | |
|------------------------------------|--------------------|
| 1. Rigid translation | 1.55-day decrease |
| 2. Decrease age to sexual maturity | 2.20-day decrease |
| 3. Decrease turnover age | 5.55-day decrease |
| 4. Decrease age at last egg | 21.00-day decrease |

In general the number of time units required to be equivalent to a given amount of increase in total fertility is smallest when the fertility is already high and the time short, whereas larger time changes are

needed when fertility is low and time long. But the general point holds true that small absolute changes in developmental rates of the order of 10% are roughly equivalent to large increases in fertility of the order of 100%.

From these considerations we should predict that very little genetic variance in development time ought to be found in species with a history

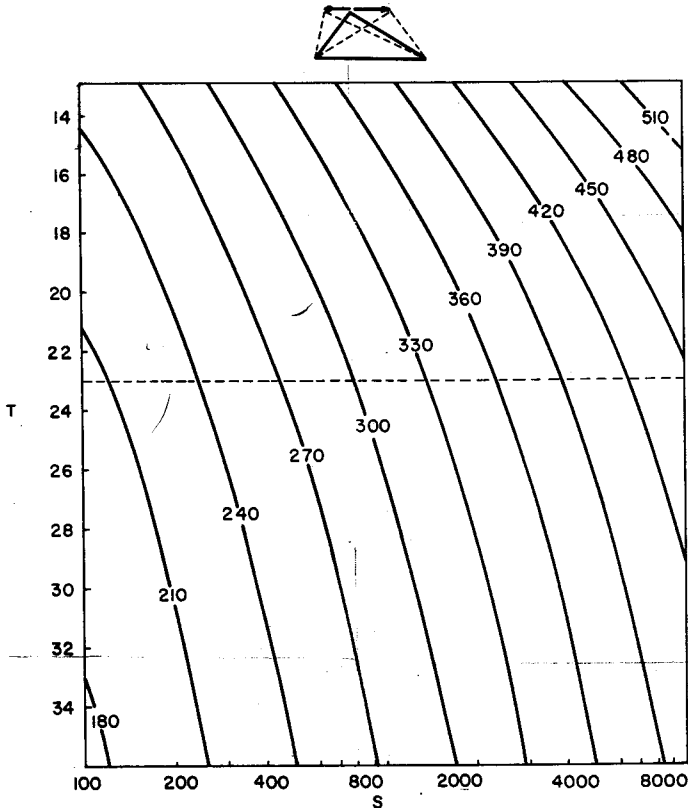


FIG. 7. Response surface showing equal r' lines for different total offspring numbers and different T values with $A = 12$ and $W = 55$.

of colonization, whereas relatively larger amounts of variance for fecundity might be expected. Selection will have long since shortened development time, but will not have acted as efficiently on fecundity. Although there is a great deal of published information on fecundities and life tables of different genotypes in populations, there is no accompanying data on developmental rates. Information from selection ex-

periments is more difficult to interpret, and no simultaneous experiments on selection for fecundity and developmental rate have been done. In *Drosophila serrata*, Birch and associates (1963) have shown that large differences in fecundity and longevity exist between different geographical races, whereas there are no differences between races in developmental rate. Tables I and II taken from that paper illustrate this point dramatically. Recent experiments of Dobzhansky *et al.* (1964) asso-

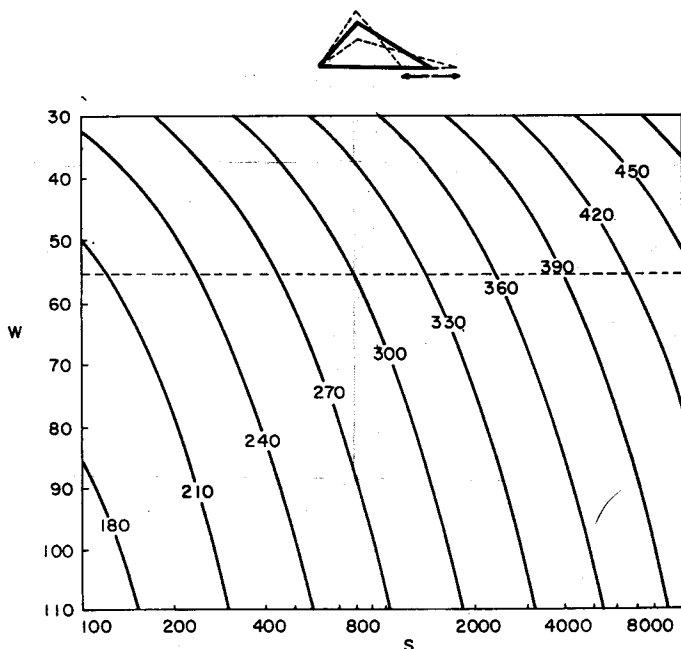


FIG. 8. Response surface showing equal r lines for different total offspring numbers and different W values with $A = 12$ and $T = 23$.

ciates in *D. pseudoobscura* laboratory populations show that polymorphic populations segregating for Arrowhead and Chiricahua gene arrangements have an average fecundity at 25°C of 431 eggs per female per lifetime. Monomorphic populations of AR and of CH give 283 and 316 eggs per female per lifetime, respectively. The polymorphic cages then produce females with one and one-half times the fecundity of Arrowhead and one and one-third times the fecundity of Chiricahua monomorphic populations. The development times for these three populations are, respectively, 13.73, 13.85, and 14.44 days, a difference between longest and shortest of only 5%.

More experimentation in this field is necessary, especially model experiments of natural selection under conditions of radical expansion and contraction of population size.

The models discussed thus far predict the course of natural selection on the assumption that the population is growing continuously in a den-

TABLE I
DURATION OF DEVELOPMENT IN DAYS
FROM EGG TO EMERGENCE OF ADULT
AT 25° AND 20°C IN
Drosophila serrata^a

Race	Temperature	
	25°C	20°C
Sydney	11.8	16.4
Brisbane	11.6	16.0
Cairns	11.7	16.1
Port Moresby	11.5	16.4
Rabaul	11.7	16.0

^a From Birch *et al.* (1963).

TABLE II
TOTAL NUMBER OF EGGS LAID PER
FEMALE AT 25°C AND 20°C IN
Drosophila serrata^a

Race	Temperature	
	25°C	20°C
Sydney	559	428
Brisbane	670	546
Cairns	498	373
Port Moresby	368	270
Rabaul	151	69

^a From Birch *et al.* (1963).

sity-independent fashion. Very soon the population will reach a size at which competition may become an important element in determining fitness and the question arises of how competitive ability is correlated with the intrinsic rate of increase, r . We know from the experiments of Lewontin (1955), Lewontin and Matsuo (1963), and others, for *Drosophila* and from the experiments of Sakai and Harper reported in this

Symposium, for plants, that competitive ability with other species or genotypes is not perfectly correlated with performance in pure stands or pure populations. Moreover, the competitive interactions appear to be exaggerated at nonoptimal densities. In the studies with Dobzhansky to which I have referred it was possible to compare the rates of increase of populations with changes in their intrapopulation fitnesses. In *D. pseudoobscura* inversion heterozygotes are usually heterotic and lead to balanced polymorphism at 25°C, but not at 16°C. In agreement with this, the rates of increase of polymorphic populations are higher than monomorphic at 25°C but not at 16°C. The agreement is not perfect however. Polymorphic Arrowhead-Pikes Peak populations have a higher r than either monomorphic Arrowhead or Pikes Peak but, in fact, there is no heterosis in this case and the Arrowhead gene arrangement eliminates Pikes Peak. In general, such results as well as the results of Sakai, Lewontin, and others show a reasonable positive correlation between performance in competitive and noncompetitive situations, but this correlation is far from perfect and there are many unique competition interactions.

The pertinence of these studies is that the selection on life cycle components that goes on during the logarithmic growth phase is not entirely lost to the population during the plateau of population size, but neither can it be assumed that those genotypes favored in the first phase are necessarily those selected during the later stages.

SELECTION IN CHANGING ENVIRONMENTS

The second question of importance for a colonizing episode is the effect of a radically changed environment. For successful colonization the population must be able to maintain a positive rate of increase at first and then, on the average, a rate of increase of zero. If the genotypes in the colonizers should be such that they fail to replace themselves, at least in the new environment the colonization will fail, the "infection" will not "take." This Symposium has given us abundant evidence of the frequent failure of colonizations, and it is certain that successful cases are a selected sample of the essentially random genetic collections that have attempted colonization. There is then a great possibility for selection between demes, selection in the characteristics of the population as a whole.

We may then inquire what the relative probabilities of successful colonization are for populations of various genetic structures and even what the *optimal* genetic structure is for a colonizer to maintain a positive rate of increase in a new environment, while at the same time maintaining itself in the original territory of the species. The same question

can be asked over time rather than space. Given a species which is reduced sharply in numbers at more or less regular intervals by unfavorable conditions, what is the optimal genotypic structure of the population which will both guarantee its survival in low numbers during unfavorable periods and also give it a high rate of increase in favorable times and allow it to maintain very large populations at peak periods? Barring trivial solutions to this problem, like perfect homeostasis, we know really very little of an exact nature.

One example of how this problem can be attacked exactly, at least in one case, is provided by the recent work of my colleague Dr. Richard Levins. Dr. Levins has been considering the average fitness of a population through time, when environmental conditions are assumed to fluctuate either randomly or with a definite period. The particular model is as follows: There is an optimal phenotype S_t which changes from generation to generation. Each genotype has a phenotype P_i and the fitness of that genotype W_i decreases as the square of the deviation of P_i from S_t . That is:

$$W_i = 1 - (S_t - P_i)^2$$

From this definition of fitness it follows that the average fitness of the population over many generations, \bar{W} , is given by

$$\bar{W} = 1 - \sigma_S^2 - (\bar{S} - \bar{P})^2 - \sigma_{\bar{P}_i}^2 - \bar{\sigma}_{P_i}^2 + 2 \text{Cov}(S_t, \bar{P}_i)$$

where σ_S^2 is the variance through time of the optimum, $(\bar{S} - \bar{P})$ is the difference between the mean optimum and the mean phenotype of the population through time, $\sigma_{\bar{P}_i}^2$ is the variance of mean phenotype of the populations, $\bar{\sigma}_{P_i}^2$ is the average within generation phenotypic variance, and $\text{Cov}(S_t, \bar{P}_i)$ is the covariance between the mean phenotype in any generation and the optimum in that generation.

This formulation shows that the average fitness of the population is decreased by fluctuating environment (σ_S^2 and $\sigma_{\bar{P}_i}^2$), but is partly restored by any correlation between phenotype and environment, $\text{Cov}(S_t, \bar{P}_i)$. This covariance is increased if the population can respond easily in its genetic composition to changing environment, but the very same genetic flexibility also increases the variance $\sigma_{\bar{P}_i}^2$ but decreases the variance $\bar{\sigma}_{P_i}^2$. The net result of all these is a balance so that an intermediate degree of genetic responsiveness may result in the highest average fitness over time. As an illustration of this balance Levins has considered, among other models, a simple one-locus case in which the phenotypic values of the genotypes AA , Aa , and aa are a , 0 , and $-a$, respectively, and in which the average value of S is 0 over long periods. As a grows larger, the population is more responsive to selection since gene effects are magnified.

The question is whether there is an optimal strength of gene effect. An example of the results of such investigations is given in Fig. 9 taken from Dr. Levins work. The different curves relating mean fitness \bar{W} to gene effect a , correspond to different degrees of correlation of environment between successive generations. We see that when successive environments are strongly correlated ($r = 0.8$ or greater) then there is an optimal

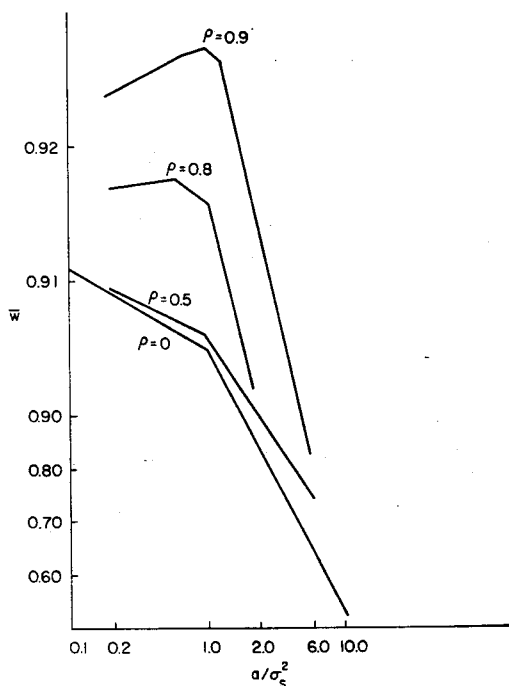


FIG. 9. Relation of average \bar{W} over time to intensity of gene effect for different degrees of serial autocorrelation of the environment. Ordinate shows \bar{W} and abscissa shows ratio of gene effect, a , to environmental variance σ_s^2 .

value of a about equal to the environmental variance. For smaller correlations, however, the greater the genetic flexibility the *lower* the fitness. Thus, it is far better in a poorly correlated sequence of environments not to try to track the environment but to have a constant phenotype at the average optimum. When environments are more strongly serially correlated, however, some genetic variance is desirable but not too much. We might expect to find that in environments with low serial correlation as, for example, environments which fluctuate every few generations, these would be strong canalization for characters in which intermediates have

the highest fitness. In environments with longer periodicities, ten-generation periodicities corresponding to a correlation of 0.8, it is of advantage to have some genetic variance and to "track" the environment.

We would predict on the basis of such work that different genetic strategies of colonization will be evolved depending upon the statistical pattern of environment. Populations with low genetic variability for a character will more often be successful in environments requiring frequent radical alteration of phenotype, whereas populations with high genetic variability will more often leave successful colonies in environments which, although radically different from the original species range, are in themselves rather stable. A note of caution is necessary here. We do not know how general this result is, but only that it holds for characters fitting the model I have described. Nevertheless, it points the way to a quantitative analysis of the problem of the genetic conditions most conducive to successful colonization.

It may be objected that examination of the optimal genetic system is not very helpful since there is no mechanism for this optimization. There are, in fact, two such mechanisms. The first is direct selection of modifiers within the population to increase or decrease the effect of a gene. That such modifiers are easily selected is well known in *Drosophila*. Second, colonizing species are being subject to constant interdeme selection since nearly all colonizing episodes end in failure. It is at the interdeme level that optimal strategies can be selected, but it must be remembered that the precision of such selection is bound to be less than for intrademe selection.

It is my hope that the methods of analysis of population strategies illustrated by the work of Levins and by Lewontin (1961) can be used generally for the solution of such evolutionary problems.

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