STABILISING SELECTION IN POPULATIONS OF DROSOPHILA

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INTRODUCTION

The general problem of stabilising selection acting on a given metrical character poses several types of question. Thus we must first enquire whether there is indeed a selection force tending to keep the mean and variance of the character constant. If so, what is the functional relation of the character with fitness? And if we can answer this question, can we identify the physiological changes involved in the decrease of fitness well enough to be able to predict the result of further change? And will we then be able to infer something of the nature and structure of the genetic equilibria which underlie stabilising selection?

We decided to follow these question step by step with the aim of formulating a model which would account for the mechanisms (both at the population and the physiological level) which are involved in stabilising selection for the particular character chosen for study, namely body size in Drosophila, which would also allow to extrapolate to the more general aspects of stabilising selection.

EVIDENCE FOR STABILISING SELECTION

For many traits in living organisms the extreme expressions are less frequent than the intermediate ones: as Galton said "the majority are mediocre". Evidence for the existence of stabilising selection has been reviewed in several papers (MATHER, 1953; BARNES, 1969) for a wide range of characters, some with obvious connections with fitness, others less so. Barnes (op.cit.) claims that sternopleural bristle number in Drosophila is a character subject

to stabilising selection by showing that deviations from the mean are followed by a reduction in the number of offspring produced. Kearsey and Barnes (1970) and Barnes and Kearsey (1970) and Killick (1970), although agreeing generally with this view, say that there are no differences between the mean value of a population and the extremes, as far as the number of offspring is concerned but, by varying the competitive conditions in the culture they found evidence for strong selection pressure in population cages which reduces the variance of bristle number, i.e. individuals belonging to the tails of the distribution have less chance of survival than the ones nearer to the mean. Latter (1958) had already shown that selection away from the mean for bristle number reduced the competitive ability of the flies, when they were grown in mixed culture with a standard marked genotype. However, although back selection had an immediate and marked response, showing that the selected lines possessed a good deal of genetic variance, relaxation of selection under the competitive conditions present in a population cage was not effective in bringing the mean value of the character to the unselected level (Alan Robertson, 1967), leading this author to conclude that sternopleural bristle number is not subject to stabilising selection and so has no functional relationship with fitness; it is a trivial character. Thus, with respect to changes in bristle number there is a sharp cleavage of opinion. We shall return to this controversy later, after dealing with our evidence.

The existence of stabilising selection has also been inferred from the behavior of the trait when artificially selected: to Thoday (1958)

and Mather (1953) the existence of large amounts of "hidden" genetic variability and the typical values of the character for different populations of the same species implies a history of stabilizing selection. This view is opposed by Alan Robertson (1956; 1964) who argues that stabilising selection, based on either heterozygote advantage or on a causal relationship between fitness and metric deviation will both produce the same end-result and consequently the inference made by Mather and by Thoday may well be incorrect.

Let us now turn from acharacter whose connections with fitness are dubious and probably not very intense to characters intimately associated with fitness, namely reproductive fitness. Darlington and Mather (1949) state that litter size in pigs has an intermediate optimum and Perring (cited by Kearsey and Kojima, 1966) quotes the same conclusion in relation to clutch size in swifts. In relation to egg production in Drosophila Forbes Robertson (1957) found little response to selection for high or low egg production - a consequence of the low level of additive genetic variance exhibited by this character. Kearsey and Kojima (op.cit.) found that dominance and dominance interaction effects were very much part of the genetic architecture of egg hatchability therefore probably not subject to stabilising selection in agreement with Forbes Robertson's earlier interpretation on the genetic properties of egg production (Robertson and Reeve, 1952). One would expect this type of behaviour in characters which are part of reproductive fitness since they have been selected to the maximum possible thereby exhausting the additive genetic variance.

Let us now consider an apparently intermediate type of character in Drosophila, namely body size. We know on the basis of Forbes Robertson's work (1957) that there is a positive phenotypic correlation between adult body size and egg production. We also know that although adult body size can vary widely there is a minimum larval size called critical size, which must be reached to allow development to be completed; it occurs earlier in the third larval instar and is probably associated to some major change in the hormonal state of the developing individual (Bakker, 1961; Forbes Robertson, EC. Gen. no.3, 1960). In this way body size is an important component of viability - the smaller the size at pupation the greater the pupal mortality (Sang, 1949). The third way in which body size is connected with fitness is through its connections with development time: every individual must reach a minimum size to be able to reach adulthood no matter how long it takes to do so. Kearsey and Kojima (1967) point out that body weight is governed mainly by chromosomes with additive effects and additive x additive interactions which is the type of genetic structure one would expect from a character subject to stabilising selection.

With regard to sensitivity to environmental variation both bristle number and egg-production are affected (through body size in the sense that both exhibit a high phenotypic correlation with this trait (Gibson et al., 1961; Forbes Robertson, 1957). Thus, the level of expressivity of very different characters like bristle number and egg production may be affected

by pressures exerted during growth. Adult body size being the end-result of growth is extremely dependant on environmental restrictions of all kinds of which the main one is probably food supply both in quantity and quality; others include temperature, humidity etc. (Forbes Robertson, EC.Gen.1-6, 1960; Sang, 1949). The results of such restrictions are expressed in alterations of the major parameters of fitness: development time, egg production and viability.

Alan Robertson has repeatedly pointed out (1963 etc.) the need for a theory of selection based on the whole genotype (or phenotype) instead of individual characters. Obviously characters are abstractions of the mind showing variable degrees of correlation with each other depending on the "sphere of influence" of the genes controlling them. However, some workers have been trapped into the sterile discussion on the semantics of "to have or not to have adaptive value" instead of trying to find what part is played by the character in the living system both developmentally and physiologically and how variation in the character can affect the reproductive performance of the individual. Naturally the detection of a statistical association between a character and fitness is an important step but in itself it does not introduce any new light on the causal relationship between the two.

Granting the need for a selection theory based on whole genotype or phenotype it is still true that some characters are more abstract than others in the sense that some more closely represent the interaction of whole genotype with environment than others. In this sense we propose that body size, insofar as it is the result of growth, with its intrinsic connections with characters

like development time, potential egg-production, viability and metabolic traits and its level of expression throughout development, represents, at the present moment, the best practical index of total integration of the genotype or phenotype. Many characters are correlated with body size in the adult stage and many others are probably associated with it during various stages of development. Many genes are likely to influence growth at one stage or another in the same way that growth parameters are likely to be affected in the same way by different genes or combinations of genes.

This raises the likelihood that such characters with a large store of additive genetic variation will respond to selection in physiologically different ways, as the deviation from the unselected level increases: in other words, the physiology of the response to selection may be different from generation to generation. There is some evidence that this is true for selection for large body size in Drosophila: Forbes Robertson (EC.Gen. No.2, 1960) found that in one selection experiment the increase in development time (measured under unrestricted feeding conditions) that accompanies this type of selection was almost entirely realized by the 2nd generation, suggesting that the response up to this stage is probably consequent upon an increase in critical size which would cause an extension of development time. Thereafter presumably other sources of variability were exploited to maintain a steady heritability. These could involve feeding rate or efficiency of food conversion. The order in which different types of variability with an outwardly similar effect on adult body size are

exploited will depend on the frequency and properties of the genes concerned. Fixation will occur for different kinds of genes at different times and hence back selection or relaxation will act on different types of variability with different effects on the growth pattern and hence on competitive ability and on fitness. In other words, the further away we are from the level of unselected population the less likely it is that a return of the selected lines to the unselected level will exploit the type of genetic variability present in the unselected population and used in the response forward.

Having considered the genetic evidence available for stabilising selection we turn now to the evidence on body size of Drosophila. Forbes Robertson (1955) showed that lines selected for large and also small body size in 4 different natural populations of D.melanogaster did not revert to the mean value on relaxation even when genetic variance was present as proved by the response to back selection. The greatest reversion was found when selection was relaxed under competitive (restricted food) conditions. In all the populations tested, artificial selection conduced to a mild decline of overall viability, under restricted feeding conditions, the decline being greatest in the low line. Frahm and Kojima (1966) also found that relaxation of selection for body weight of D.pseudoobscura had no effect in bringing the character back to its unselected level, even when relaxation was conducted under widely different selection pressures. These results are in perfect agreement with Forbes Robertson's results. Two important

points must be made at this stage: firstly all these relaxation experiments were conducted under pure culture conditions, in which each individual in the group is competing with its own kind and not, say, members of the unselected population. This could well be one of the factors responsible for the apparent stabilization of the relaxed selected lines at values different from the one characterizing the base population. The second qualification arising from the point just made concerns the physiological mechanisms which underlie the response to selection for body size. For example a given increase in size can be brought about by an increase in critical size, an increase in feeding rate or in the efficiency of food conversion (Forbes Robertson, EC.Gen.Series; Church & Robertson, 1966).

THEORETICAL MODELS FOR STABILIZING SELECTION

Sewall-Wright (1935) stated that in most metrical traits the best adapted individuals were probably the ones nearest to the average. He studied the correlation between the values on the scale of a metrical trait and a scale of fitness under different conditions of genetic control: complete or partial dominance, epistasy and also environmental effects. He found that in a population whose mean coincides with the optimum value, the parental-offspring and fraternal correlations in fitness are approximately the squares of the corresponding correlations with the character itself, independent of environmental complications. This is usually called the quadratic model in which fitness falls off as the square of the deviation from an optimum value. Falconer (1964) has also considered this idea in the broad context of the genetics of correlated characters. Several authors improved Wright's

model subsequently, amongst whom Kojima (1959) who demonstrated that stable equilibria could be attained provided the character showed partial or overdominance. Jain and Allard (1965) reached the conclusion that optimizing selection based on the quadratic model appears to be favourable to the long-term maintenance of genetic variability, even in undivided populations, although this effect will be reinforced by subdividing the population into partial isolates. Singh and Lewontin (1966) disagree with the previous authors on the role played by linkage on the stability of the equilibrium reached under stabilizing selection. More recently Gale and Kearsey (1968) and Kearsey and Gale (1968) criticized the elaborations of the quadratic model on the grounds that all these models required a fairly large degree of unidirectional dominance in the character concerned; and this conflicts with the genetic structure of many characters under stabilizing selection, which are controlled by genes showing weak ambidirectional or no dominance. These authors point out that, provided the genes that control a given metrical character have different effects on it, stable equilibria may be reached provided a balance is attained between the degree of linkage of the genes and its effects on the character. Also Barnes and Kearsey (1970) infer that their data on sternopleural bristle no. does not fit the quadratic model but is in agreement with the linear model proposed by Gale and Kearsey (op.cit.).

Alan Robertson (1955; 1963) developed the consequences of the functional relationship of a metrical character with fitness in terms of

1) in heterozygote superiority (Lerner, 1954) or 2) a causal relationship of the character with fitness in the sense that phenotypes deviating from the mean would be physiologically or developmentally less fit than the average ones. The conclusions drawn from this study are that the last situation will lead to fixation of one of the alleles at the locus under consideration. The alternative hypothesis will have as its consequences the preservation of genetic variability at the expense of the fitness of both homozygotes (the extreme deviants). In this last situation, inbreeding from the extremes of the distribution, from selected lines or from the mean will have exactly the same effects on fitness compared with the other situation in which the results will differ for inbred lines drawn from the centre of the extremes of the distribution. The value of this model is that it makes specific predictions concerning the behaviour of fitness in a given experimental situation and as such it will be discussed later in connection with our own results. Latter (1960) developed Alan Robertson's model further by considering the effects of relaxing selection under the two genetic models considered by Alan Robertson and found that relaxation will conduce to exactly the same results for both models thus reinforcing Alan Robertson's idea that the same functional relation with fitness can be based on quite different genetic situations leading to different destinies.

TOWARDS A PRACTICAL DEFINITION OF FITNESS

Now that we have looked at the evidence for stabilizing selection and the genetical theories proposed to explain it we must consider how we propose to measure fitness in experiments designed to study stabilizing selection for body size in D.melanogaster. We must realize at once that the measurement of fitness, generally speaking, is a function of the problem under study. If we do not concern ourselves, for the time being with complications such as the geographic dispersal of a population, its degree of genetic isolation and the degree of integration of the genes within a population we can imagine two types of situation which we can refer to in terms of colonizing and non-colonizing species.

Lewontin (1965) claims that colonization may be defined as the establishment of a species in a geographical or ecological space not occupied by that species and argues that it is better to speak of colonizing "episodes" rather than colonizing species since a species may colonize repeatedly the same space in different times, say, every year. Species which often experience colonizing "episodes" compared with others which do so much less frequently will be referred to here as "colonizing species" and include such species of Drosophila as melanogaster, simulans, pseudoobscura serrata, willistoni etc. All have an enormous potential of growth (reproductive rate) which is intimately dependent on the environment, i.e. on the flow of energy from the environment into the population. The environment, taken in this sense as the supplier of energy (food + temperature) to both larvae

and adults, has powers of control over the productivity (larval biomass) and egg production, by increasing development time and reducing size and potential egg production in the 1st case and by reducing actual egg production through a reduction in the level of feeding of adults. The result of this is that there will be opportunity for a quite high intensity of selection operating during both larval and adult stages. Since different genotypes are likely to transform energy in different ways there will usually be a great excess of flies or eggs produced in relation to the number needed to keep the population size constant. Colonizing species sensitivity to environmental conditions makes them perfectly suited to widely varying environmental conditions. One knows that each winter population size is drastically reduced and in the beginning of spring population size begins to increase reaching a maximum sometime during the summer and decreasing thereafter to another minimum in the winter. The growth of the population follows probably the increase in the food supply and the raising temperature. Selection pressures follow probably a continuously increasing curve, since, in colonizing species, competition is mainly for food with its consequences on productivity and will be density dependent.

At the other extreme we find non-colonizing species like D. disticha (Forbes Robertson et al., 1968) and others whose productivity is not density-dependent. In fact such species produce very few offspring whose fitness is probably dependent on their success in finding the right type of food rather than its quantity and in avoiding destruction by predators. In our discussion of competition we shall be concerned only with so-called colonizing species.

COMPETITION

The designation of a competitive index poses problems due to our ignorance of the ecology of Drosophila. If we wish to apply such an index to different populations we find that we do not know the mobility of members of a given population, the variety of niches available to different populations, levels of migration or the process of colonization which must occur regularly in a species like D.melanogaster. Ideally we should like to have a measure of the genetic differences between populations which are relevant to adaptation. Some data on "coadaptation" of genes within populations already exists and will be discussed later.

Accepting that any statements about competitive ability under natural conditions may be premature, we can nevertheless discuss the criteria for interpreting competitive ability in the light of laboratory experience. Many workers have considered competition between members of a population and a standard genotype, easily recognisable phenotypically due to the presence of a mutant gene. Such comparisons provide estimates of relative fitness (KNIGHT and ROBERTSON, 1957). This approach has also been extended to comparisons between species (BARKER, 1970; HELW and AL, 1970; TANTAWY and EL-WAKIL, 1970). One criticism here is that we are dealing only with the final outcome and no attention has been paid to the growth patterns which will influence the competitive ability during larval growth. Some attention has been paid to the competitive relations between adults by taking account of mating ability, egg production and

competition for oviposition sites (Latter, 1958). One feature of earlier studies is that development time has been disregarded as a major component of fitness, or when it has been considered, differences in adult body size have been ignored, although such differences, being correlated with potential egg production are clearly important (Forbes Robertson, 1957). Thus most of the earlier studies of competition have not attempted to dissect the basis for any apparent difference in competitivity in terms of the physiology of growth, hence it is not surprising that at present we are unable to predict the outcome of competition between any two strains. Let us consider the possibility of taking a more positive stand.

The choice of a suitable index of competition depends very much on the particular problem under study, such as intra vs. inter specific competition. If we are concerned with the stability of the mean of metric characters we are concerned with competition between individuals of the same population. For purposes of comparison it is convenient to create a sub-population carrying a genetic marker which does not substantially alter the growth pattern. On the other hand, if we are concerned with defining competitive ability between members of different populations or related species, then we can hardly expect to extrapolate confidently from comparisons between small numbers of population which are likely to be subtly different in growth patterns in the manner of Ayala, 1970.

It is proposed here that the best operational definition of fitness for a species like D.melanogaster is productivity or biomase per

unit of time. This concept was used by Carson (1957) although he applied it only to pure cultures. The advantage of this criterion is obvious when we bear in mind the connections between body size, egg production and development time. Several other definitions of fitness have been proposed like Lewontin's (1957) - the general adaptation of a population qualified by the number of specific environments in which the population can survive and reproduce. This definition is open to the obvious criticism that the number of environments is unknown and unknowable. The same criterion applies to Thoday's fitness - the probability of a population leaving descendants after a given period of time, such as 10^8 years.

Although a criterion of fitness in terms of biomass per unit of time is useful in practice and extremely valuable as a measure of adaptedness of a population to its niche it suffers from the defect that we know nothing about the correlation between competitive in mixed culture ability and productivity in pure culture. It is quite conceivable that low productivity in pure culture may go along with greater competitive ability in mixed culture with a strain with high productivity in pure culture; there is in fact one case in the literature where this seems to happen (Gale, 1964).

Lewontin (1965) studied theoretically the relative importance of three components of fitness in a colonizing species, development time, fecundity and longevity, and found that during the colonizing period when population size was increasing, development time is by far the most important. This is quite independent of the restrictions imposed on egg

laying and viability through changes in the ecology like the ones found by Sang (1949), Latter (1958) and Kinross (1969). These authors agree that the viability of eggs decreases as the age of the culture increases up to a certain limit; generally speaking the only viable eggs in population cage or bottle conditions are the ones laid in the 1st couple of days. The reasons for this will be examined later in connection with experimental and simulation data. What we must bear in mind at this stage is that colonization of a niche by D.melanogaster is "instantaneous" i.e. only the eggs laid in the first couple of days have a chance of reaching adulthood no matter how long the laying adults remain in contact with the culture. The relevance of this phenomenon will no doubt be appreciated later on.

Competition probably represents the best approach to the study of such problems as the maintenance of single-locus polymorphisms or stabilising selection in the case of metrical characters. Once we have created a suitably marked sub-population and defined a suitable level of competition we are then able to make predictions concerning the productivity patterns of the sub-populations competing against our marked population, provided we know the way in which the physiological parameters are altered in these sub-populations. Turning the argument the other way around, for practical purposes, we may be able to infer from the competitive relations which physiological parameters

conditions are altered (by varying the level of crowding, the frequency of the competing genotypes and their age structure). This is broadly speaking the path we shall try to follow in our experimental approach to the problem of stabilising selection for body size. But we must remember that fitness, or competitive ability, of a genotype does not depend only on the difference in competitive ability between the two competing strains. It also depends on the ecological situation created by members of these strains according to their physiology and the frequency at which they are competing if they are different.

There is a considerable body of literature covering the topic of variation in fitness as a function of the frequencies of the competing genotypes: this is usually referred to as the "frequency-dependent" selection model. Most of the papers were published after Kojima and Yarborough published their papers in 1967 showing that the rarer genotype was always at a relative advantage over the other competing genotype. Since the papers by Lewontin and Hubby in 1966 had shown the existence of high levels of heterozygosity in populations which could not be explained solely by heterozygote advantage, it was felt that some other mechanism might be involved in the maintenance of polymorphisms in a population. Frequency-dependent selection seemd to be one good enough for the purpose not only on account of the intellectual and aesthetic appeal but also because it had been previously studied by Teissier (1954) and also by Levene, Pavovsky and Dobzhansky (1958) in connection with chromosome inversion polymorphisms. Also Lewontin (1955) had found that the survival of a certain genotype in

mixed culture depended on the genetic composition of the culture. Thus the idea of frequency-dependent selection is not new; neither is Gause's principle (Gause, 1935) which states that if two species are forced to coexist in an undiversified environment one inevitably becomes extinct and if two species do coexist they must occupy different ecological niches. This principle is as attractive as the frequency-dependent one; but how does one reconcile one with the other? Or must we choose between one of them?

It is of interest to consider how far Gause's principle is relevant to intraspecies competition. Where two genotypes compete for a single generation, before gene exchange can occur, the intraspecific situation is formally analogous to the interspecific and any tendency to maintain per-time assortative mating will extend the analogy. But when gene exchange can occur, a new situation arises, due to segregation of genes which control physiology and behaviour, and we should then have to consider the model in relation to frequency of genes which are so consistent in their expression, in spite of segregation in the genetic background, that the possibility of one displacing the other could be envisaged. Obviously if frequency-dependent selection occurred, this would represent a special departure from the Gause principle.

As we stressed previously our poor knowledge of the ecology of D.melanogaster prevents us from being fully confident of selecting all the

right ecological parameters under which to study competition. Although we do not know what constitutes exactly a niche in Nature, we can accept that every niche must have two basic dimensions - space and time. Although larvae of Drosophila exhibit the "scrambling" type of competition (Nicholson, 1957) it is likely that each larva has a certain sphere of action or movement and that its competitors at a given time, will be mainly the larvae present inside this sphere. In any culture there will always be variance in body size and therefore variance in biological age, resulting from genetic variance in growth rate or from variance in the age of the eggs laid at the start of the culture. The consequence of this variance in biological age is that the competitive conditions will vary considerably with the age of the culture, not only because the potential food supply is affected but because the crowding will vary as individuals are removed from the medium by pupation or death. Therefore we may have quite different genetic compositions in the culture at different times.

After space and time we can make a further restriction on the ecological determinants of fitness by saying that under the conditions usually met with in the laboratory - uniform temperature and food quality - the basic selection factor is food shortage. This restriction may perhaps be easily extrapolated to natural conditions, bearing in mind that other factors, some known, like temperature, and some unknown are likely to be very important as well. If we imagine two species or genotypes with the same fertility

simultaneously colonizing a given niche, but having different speeds of development and if such niches are randomly distributed in space and time it is obvious that the slow developing species or genotype will be rapidly eliminated.

The argument based on the fact that different proportions of two different growth types can lead to different selection pressures inside the culture must certainly lead to the conclusion that the overall productivity of the culture will vary with variable genotypic structures, in the same way as different crowding levels originate different productivity. If two cultures with different genotypic ratios, consequently with different selection coefficients attached to each of the genotypes and different overall productivities, are faced with the task of colonizing a given space, one of the cultures will provide more individuals than the other, at a frequency that in itself will be at an advantage over the frequency prevailing in the other culture. If this happens we have a basis for considering the connection between the fitness of individuals and the "fitness of frequencies" or populations. There are naturally many difficulties attached to this concept but it may be of interest to consider this in connection with the stability of gene frequencies with environmental fluctuations; however it is clear that it has immediate use when we are considering competition between species.

Several authors have studied competition between different colonizing species of Drosophila (Barker and Podger, 1970; Miller, 1964; Tantawy and El-Wakil, 1970; Ayala, 1969, 1971) using different ecological systems. Generally speaking they were unable to predict the outcome of competition on the basis of the results from pure cultures. None of the ecological systems used was designed to reproduce the conditions met by the competing species under natural conditions nor were important productivity parameters like development time taken into consideration. This evidence will be considered later.

COMPETITION AND THE GROWTH MODEL

Now that we have looked at the general possibilities and limitations of a competitive test as an indicator of fitness it is time to consider the growth model which underlies our attempts to explain competitive ability in terms of the physiology of growth, which allows us to predict competitive ability once we know the physiological characters of the strains involved.

The model described here as a basis for physiological interpretation is based on the work of Bakker (1961) and Forbes Robertson (EC.Gen., 3, 1960). It is convenient to divide the growth of D.melanogaster into two parts. The 1st or precritical stage extends to the early third instar when the larval weight is about half its final value and so covers the exponential phase of growth. The second period extends from the critical stage until pupation. The critical size corresponds to an important phase in the hormonal relations

which govern growth since, after this stage is reached, the larvae can pupate even although deprived of food, whereas before this stage they cannot do so. Also the interval of time between attainment of the critical size and pupation appears to be more or less constant and independent of diet whereas low levels of food may indefinitely delay the attainment of the critical size. Bearing in mind the variation in time to reach the critical size versus the relative constancy in time during post critical and pupal life, we can define certain restrictions and interpretations of observed differences in growth in pure and mixed cultures.

Individuals with the same development time have the same competitive ability since phenotypic variation in body size in a nutritionally sub-optimal environment is chiefly a consequence of the food available during the later growth period. Flies of the same development time will be of the same size unless there are other causes of variation. If the latter exist and cause variation in spite of similarity in development and larval competitive ability this could arise in the following ways.

The critical weight may differ between individuals. Forbes Robertson has shown how this may be changed by selection under certain defined conditions. If this effect occurs, a slow growing individual could hatch at the same time as a fast growing one under competitive conditions if the latter had to reach a larger critical size. This leads us to consider the nature of the growth rate which can be altered by change in

the efficiency of food conversion, given a constant food input, or by alteration in the rate of feeding or appetite, with or without a change in the efficiency of food conversion. We shall ignore hypothetical causes of variation in competition such as excretion of wastes into medium which differentially effect the growth of genetically different individuals. (Dawood and Strickberger I and II, 1969; Weisbrot 1966).

To elucidate the first point - the possible differences in critical weight - we need to study competition between individuals with a largely common genetic background. If average body size and development time are the same under optimal conditions, it is highly likely, on the basis of earlier experimental evidence (Church and Robertson, 1966) that the critical size will be the same. In species comparisons, however, we must recognise the possibility of a relative shift of the critical stage along the growth curve in spite of comparatively small differences in total development time (Royes and Robertson, 1964).

With regard to variable efficiency of food conversion, under our kind of competitive conditions, lower efficiency will lengthen development time by ensuring a longer time to reach the critical size, and will probably reduce adult body size as well, if the values of efficiency for the two periods are correlated. In competitive situations increase in efficiency of food conversion will be an advantage and lead to differences in development time between strains which are inherently different in this respect.

An increase in feeding rate will on average favour an increase in competitive ability. Under sub-optimal conditions an increased feeding rate will lead to a reduction in development time, but not below the unrestricted feeding level, and possibly an increase in final body size while a decrease in appetite will lead to an increase in development time and to a smaller size, although it does not necessarily follow that the reciprocal relations will hold although they may do so.

These considerations have to be related to the ecology of the culture, especially the amount of yeast available to the growing individuals at different stages of larval growth. The competitive conditions in our tests differs from that in a population cage since the adults are not in contact with the larvae while the number of eggs in a culture is initially fixed, as well as the initial amount of yeast. Also the amount of substrate for yeast growth is fixed at the start of the culture's life. Growth of individuals will be influenced thereafter by the quantity and quality of the food available. The growth of the yeast population from a constant initial size is a function of the way it is "cropped" as well as the basic nutrient supply. Under competitive conditions the cropping rate is probably the major determinant of yeast growth while larval growth rate is a function of the concentration of yeast cell in the medium and their nutrient quality. If the system had some self-regulating properties this would reduce the rate of "cropping" until the yeast population had recovered. One simple feed-back system would operate through the

death of those individuals who do not eat enough for their maintenance. This would tend to reduce variation between individuals in adult body size but if this does not happen, as is almost certain, then the food supply will tend to diminish as the culture ages leading to extension of development time and reduction of body size, according to the size of the initial yeast population, the density of larvae, etc. A light cropping of yeast will obviously have mitigating effects.

Assuming that the way in which the fly population exploits the yeast population is genetically determined in part, different methods of exploitation may lead to similar results in terms of biomass per unit time. It would be easy to diversify the model with additional qualifications, e.g. death of less well adapted individuals in competitive conditions. An early mortality rate in competitive conditions would benefit the survivors while a low mortality rate at the beginning would create more unfavourable conditions later, hence levels of sensitivity and death risk at different stages could play a role in adaptation.

It should be clear from these considerations why we cannot predict from the productivity of a given strain its performance under competitive conditions unless we know more about the physiological factors which determine success in competition. What are these factors?

Generally speaking they are critical size, efficiency of food conversion and appetite. They may or may not be genetically independent

and their interdependence may well interact with the environment. Let us consider the ways in which each of the parameters varies and the consequences for the competitive ability of the individuals and the productivity of the cultures.

Critical weight: It is known from previous work that critical weight is variable both between species (Royes and Robertson, 1964) and within species (Church and Robertson, 1966). Royes and Robertson showed that species with similar body size such as D.funebris and D.immigrans have nevertheless different critical weights. The higher survival of D.melanogaster when competing at high levels of crowding with D.simulans suggests a higher critical weight for the latter, although there is no difference in size between the two species under optimal conditions (data from Miller, 1964). In such cases there is a shift of the critical point along the growth curve, raising or lowering the critical weight, increasing or decreasing the duration of the exponential growth period and reducing or increasing proportionally the post-critical phase. This shift introduces a source of variability between species of Drosophila in the growth pattern, and is a very important factor when considering interspecies competition. In intraspecies competition we shall take for granted, on the basis of extensive evidence collected by Bakker (1959, 1969), Forbes Robertson (EC. Gen. No.3, 1960) and Church and Robertson (1966) that although ther is variation in the critical weight and in the associated duration of the precritical period, there is little variation in the duration of the

post-critical period, in spite of variation in food supply. In other words the shift of the critical point along the growth curve is not followed by a compensatory change in the duration of the 2nd period. What are the consequences of an increase in critical weight on competitive ability and productivity? It is obvious that both parameters will decrease, with an increase in development time. Under optimal conditions there will be an increase in development time as well as in body size, all other things being constant. A decrease in critical size will have the opposite effects.

Forbes Robertson (EC.Gen.No.2, 1960) found that selection for body size in live-yeast cultures generated a slight increase in development time and that the increase was realized very early in the selection, suggesting that the factor responsible for much of the response to selection in the early generations was the genetic variability of the critical weight; this would be a factor responsible for natural selection against progressive increase in size. Selection for small body size, however, did not reduce development time suggesting that the factors involved in the response were other than changes in critical weight. We would expect this to happen since natural selection must have acted to bring it down to a minimum.

One point to be noted concerns the variability of critical weight due to environmental causes. Selection for body size under different nutritional conditions generates responses based on different physiological

pathways and possibly different critical weights (Forbes Robertson, EC.Gen, 6, 1963). Church and Robertson (1966) state that the ratio of DNA content at critical size to that of the adults is virtually constant, while the corresponding ratios for time and protein content vary, although not greatly. This shows how variation of protein content at the critical point can be the cause of variation in critical weight. It is not difficult to imagine a component of body size other than protein, e.g. fat, which generates this variability mainly when the flies are grown under unrestricted conditions. This possibility will be considered later in relation to regulation of growth. Forbes Robertson (EC. Gen. 6, 1963) studied the growth pattern of flies fed under restricted conditions for a variable period and then transferred to unrestricted conditions. One knows what the critical weight is for flies grown under optimal conditions; so if we use this estimate to time the occurrence of critical weight in larvae grown under restricted conditions we can then predict what the effects of transferring these larvae to optimal conditions will be. We'll expect that the earlier in the 2nd period they are transferred to the smaller will be the deviation in size from the controls fed on optimal diet all the time. Assuming that post-critical growth has a constant duration (it was estimated by Forbes Robertson to be 42 hours for the standard temperature conditions) it is clear that larvae grown under low protein (axenic) or crowded (live yeast) conditions either reach critical point at a higher weight or have a delayed 2nd period of growth.

With respect to the 2nd parameter, efficiency of food conversion, defined as the fraction of biomass gained per unit of food ingested, we can see that an increase in efficiency will be translated into an increase in competitive ability and vice-versa. Parallel changes will be expected for productivity with a reduction in development time in the 1st case and an increase in the 2nd. There may or may not be changes in body size under optimal conditions in the same way as there may or may not exist changes in development time due to the high quality of the food. It is unlikely that there will be a reduction of development time with an unrestricted food supply for the same reasons that we gave for critical size.

Obviously any changes in efficiency may have its causes in differences in the metabolic capacity of the individuals (genetic) or may be a function of the quality or quantity of the food ingested. It is not difficult to imagine a bell-shaped curve describing the relationship between efficiency (ordinate) and food-input (abcissa) with an optimum input/unit of body weight. Also a relative deficiency in one of the components essential to assimilation may well affect efficiency, just as say, a proper Calcium/Phosphorus balance is necessary for an efficient mineral conversion in some mammals. We would expect that efficiency would have been maximized by natural selection taking into account the variety

of environmental circumstances the species has experienced; this means that we may find increases in efficiency in relation to some particular environment but this increase may well be negatively correlated with performance in other environments.

The 3rd parameter is appetite, a behavioural trait. An increase in appetite will lead to a higher competitive ability but will also mean an increase in the intensity of competition and therefore an increase in development time. A decrease in appetite will have the opposite effects. Body size will probably be increased in the first case and reduced in the 2nd. Development time is likely to be affected in both cases.

MATERIALS AND METHODS

1. STOCKS

Our experiments were confined to D.melanogaster. The base population for most of our studies was the Pacific wild-type population which is descended from wild flies and was kept in a cage for many years before the start of the experiments.

In the beginning of 1970 a white-eye population was initiated by backcrossing a white-eye gene into the Pacific background, several times and then letting it propagate freely in a cage. It was assumed that the differences between this population and its WT counterpart had been reduced to the white-eye gene and a bit of chromosomal material on either side of it. This population was used for the majority of the competition experiments described in this thesis.

In the spring of 1970 a W^{ap} (apricot) mutant was isolated from a line which had been selected for small body size for two generations. This mutant was backcrossed into the unselected population and then propagated in a cage. Since this mutant arose spontaneously it represents valuable material for future competition tests, because the differences between it and the Pacific wild-type populations are limited to a single gene.

In our coadaptation experiments we studied the results of crosses between the Pacific and the Kaduna populations and the results of competition between these populations and their white-eyed counterparts.

The Kaduna WT population (NK) arose from flies captured in Northern Nigeria and maintained in population cages for the past 20 years. The Kaduna white-eye population (WK_2) arose from the previous one and from the white-singed mutant and has been run in a cage for the past 8 years.

2. TYPES OF CULTURE

Unrestricted feeding conditions (also referred to here as optimal conditions) - The food in these cultures consists of 5 ml. of the ordinary maize meal-molasses-agar mixture reinforced with a lump of thick fresh yeast paste supplied by Distillers Company Ltd. This food is supposed to provide the growing individuals (70 eggs per vial) with an excess of all the food requirements that they need. Ordinary size vials were used., measuring 8 cmx 2 cm.

Restricted feeding conditions (also referred to here as competitive conditions) - The medium utilized in these cultures is basically a dilution of the above medium and is made up as follows:

75 g of maize-meal
50 ml molasses
10 g of agar
1000 ml of water

Small cylindrical vials are used as containers, measuring 5 cm x 1 cm. Each vial is filled with 2 mls. of the medium and a drop of diluted live yeast suspension on the surface of it.

Crowding tests using a standard amount of this medium and a variable number of eggs enabled us to plot the average body size against the initial number of eggs. From the regression line fitted and from the measurements of body size in the population cage we can determine which level of crowding corresponds to the average intensity of competition in the cage. We have concluded (see Fig.1) that for our Pacific population this level is 30 eggs/vial. A full discussion of this experiment will be presented later. Meanwhile we must point out that another important conclusion drawn from this test is that the feeding conditions provided by our competitive medium are sufficient to enable growth to a level comparable to growth under optimal conditions, provided the crowding level is low enough. This conclusion is substantiated by further experiments where the larvae were grown under competitive conditions for variable periods of their life before an excess of fresh live yeast was added to the cultures: whenever this yeast was supplied early enough (not after the larvae reached the critical stage) body size reached its optimal level, thus proving that the restriction in food was mainly a restriction in the supply of yeast.

3. CHARACTERS MEASURED

Body size - The parameter chosen was thorax length, which is measured with the help of a microscope and a scale in the eye-piece. The detailed method was described by Forbes Robertson and Reeve (1952) and consists basically of

etherizing the adult flies, placing them horizontally on a little platform and reading the scale in the eye-piece.

The values for thorax length were converted into measurements of body size by raising thorax length to the cubic power as follows:

$$b = (\log_e t \times 3) - 12.00 \times 100$$

where b is the transformed and coded body size and t is thorax length. A logarithmic transformation was used to avoid any scale effects on variances. The subtraction of 3 $\log_e t$ by 12.00 and multiplication by 100 are nothing but coding procedures. This transformation allows us to estimate percentage differences in body size by the simple subtraction of the uncoded log values.

The variance of body size of flies grown under optimal conditions was analysed with a single criterion of classification as explained in the statistical section. Differences between the average size of two competing groups of flies under competitive conditions were analysed by t-tests within days, although days were sometimes pooled, as Day 1 + Day 2 and Day 5 plus all subsequent days. No attention was paid to replicates since most of the times there were not sufficient numbers within replicates to allow this source of variation to be properly considered.

Development time - Flies grown under optimal conditions were collected twice daily, at 9. 0am. and 5. 0pm. and their development time estimated on the basis of these collections. In the competitive tests day-intervals were used, from the beginning of hatching until all flies had emerged. Usually flies were removed from the culture vials at around 5.0pm., thus avoiding any possible interference with the morning peak of emergence.

The estimator of development time of flies growing under optimal conditions is an absolute one, i.e. expressed in the average number of hours or days taken to complete development. In the competitive tests the differences in development time between the competitors are expressed by the difference within days between the numbers of individuals of each genotype. These differences are compared by the use of one-way classification analysis of variance and individual t-tests where required.

Viability - This refers to egg-to-adult viability and is expressed by the ratio of the total number of adults hatched and the initial number of eggs.

Differences in viability within a competitive test, between competitors are tested by χ^2 with expectations equal to the number of eggs at the beginning of the culture. χ^2 on totals and heterogeneity χ^2 were computed to test differences in viability and homogeneity of replicates in respect to these differences. The variance of

differences in the viability of the same strain when competing at the same time with different competitors was analysed by the procedure indicated later.

Productivity - This term refers to the total number of individuals hatched in a culture on a given day or during a certain number of days irrespective of their genotype. Productivity on a given day very much depends on viability, since a high viability will tend to decrease productivity in the early days of hatching and increase it later on.

The variance in productivity of contemporary cultures will be analysed by the procedure indicated later. Our comparisons of productivity involved single days, productivity pooled over more than one day, including the productivity of the whole hatching period. Scale effects should therefore not be very important and so no logarithmic transformations of the data were carried out before analysis.

Egg production - Forbes Robertson (1957) found a phenotypic correlation between body size and egg production in both genetically homologous stocks and random-bred populations. He also found, together with Sang (1944) that different levels of feeding of the adult individuals generated different levels of oviposition. Since both size and egg production are a consequence of the amount of food available to the larvae and to the adults, we need first of all to establish the conditions under which larvae should be grown as well as the conditions under which

adults should be fed when their egg production is being measured. We have dealt with the first part of this problem. As to the second part, there is not a uniform parameter to indicate egg-production in D.melanogaster (McMillan, 1970): Gowen and Johnson (1946) used the egg-production from the 4th to the 8th day after emergence since it was strongly correlated with lifetime egg-production. Other authors whose work was reviewed by McMillan (op.cit.) used estimates of egg production believed to be more or less correlated with life-time egg production.

In all these measurements the dominant preoccupation in the minds of the researchers was the conditions which limited the variation in body size of the laying adults (found by growing larvae under optimal conditions) and those under which the maximum laying capacity of the females could be manifested. Little consideration was given to ecological limitations which might affect development time thus altering the age at which the first egg would be laid and to the relative importance of this age when compared with the number of eggs laid. The question as to whether it is better to have one egg laid today or many laid tomorrow, was not asked until Lewontin (1965) published his valuable paper on the relative importance of different

components of fitness in colonizing species. Also little attention was paid to the way in which adult individuals of Drosophila, with different genotypes and/or phenotypes react to different levels of feeding: is there an interaction between the metabolic activities underlying growth rate and egg production?

We decided to study the egg-production of flies which had been grown under four different feeding levels, all being live-yeast systems: optimal, 10, 30 and 40 eggs per vial of competitive medium. These four levels were applied to each of the three lines studied: the unselected and the two selected lines. These lines came from the sel 2 experiment at 5 generations of relaxation from GEN 7 of selection.

Normally the adults were fed on a rich suspension of live yeast for 24 hours/day. Since food was renewed every twenty-four hours and the incubation period of the eggs is around twenty-one hours it is unlikely that any interference on oviposition from the newly hatched larvae had occurred.

It is very probable that under natural conditions the feeding regime of Drosophila is not always as good as twenty-four hours a day. Therefore we studied the effects of different feeding regimes on adults grown under optimal conditions and belonging to lines selected and unselected for body size. These lines were obtained from the sel 2 experiment at 7 generations of relaxation from generation 7 of selection. Four levels of feeding were studied. The flies were

kept in contact with the standard live-yeast food for 0, 1, 5 and 24 hours per day; in the remaining periods oviposition was allowed to continue on yeast-free agar lids. Records of oviposition were kept separately for the "yeasted" and "non-yeasted" periods of oviposition over several days.

We also conducted an experiment designed to measure the egg production of flies that had spent periods of variable duration under competitive conditions (cage level) before the conditions were made optimal by the addition of an excess of fresh live yeast.

The technique followed to assess egg production involved the following steps:

1. The flies were anaesthetized with CO_2 to avoid alterations in oviposition due to etherization.
2. Each female was allowed to lay on an agar lid in the centre of which was deposited a drop of thick fresh yeast suspension. The agar lid was mounted on a cork which was fitted into an empty culture vial containing a strip of filter paper to absorb any extra moisture and to give the flies a rough surface on which to sit. The vials were kept in an inverted position.
3. Egg production was measured for individual females. At 24 hour intervals a new lid was introduced. The old one was removed and the eggs on it were counted.

Only a superficial statistical analysis was carried out, consisting of the calculation of the mean egg-production for strains and days.

The procedure followed to collect eggs was a follows:

1. The laying females and the males were "fed up" for a period of 3 days at 25°C. Fresh DCL yeast was used and care was taken to prevent the surface of the medium becoming "ploughed up" by the larvae as this is known to inhibit egg laying.

2. Flies were allowed to oviposit overnight (5.0pm.-9.0am.) on an agar lid made of the following mixture:

Agar	8 g
Acetic Acid	1.33 g
Ethyl Alcohol	2.67 g
Water	100 ml

and partially covered with a layer of fresh yeast. This mixture simulates fermenting food, therefore attracting the flies and inducing oviposition.

3. If the eggs are going to be cultured under optimal conditions the eggs laid overnight can be used for this purpose. If, however, we need eggs for competition tests, we want to minimize the variance in the age of eggs, caused by the long laying period and by intra uterine embryonic development. In order to achieve this we must collect eggs for a shorter period, say 2 hours.

4. ECOLOGY

Not much is known about the ecology of D.melanogaster. In the laboratory the usual ecological systems chosen are vials, bottles and population cages. All of them utilize the same type of food - maize meal-molasses-agar - which turns out to be a good substrate for growth of a yeast population, the main source of protein and nucleic acids, needed for Drosophila growth. Any population geneticist will say immediately that the effective population size increases from vials to cages and that the population cages are the closest approximations to natural conditions. This opinion will be discussed later.

There is a substantial body of literature concerning the growth behaviour of D.melanogaster under a wide range of qualitatively and quantitatively nutritive situations (Sang, 1956; Forbes Robertson, EC.Gen.series). From these experiments we learned that growth of Drosophila is sensitive to shortage of some metabolites and that strains of Drosophila, unselected or selected for body size or for development time under live-yeast conditions interacted with the environment when grown under restricted conditions. Also, strains selected for body size or development time under restricted conditions show variable degrees of correlation with their performance under unrestricted live-yeast conditions.

All this work was done under sterile conditions unlikely to occur in Nature where "contamination" by several types of microorganisms

is the rule. Drosophila is always found associated in Nature with yeast on which Drosophila females depend as a source of food for egg-laying and possibly as a sensory stimulus for oviposition. This dependance is not restricted to the adult stage: it extends to the larval stage as well, where the speed of growth is a function of the amount of yeast present in the normal laboratory cultures (Sang, 1949). This is also probably true for the rotten apples which Drosophila individuals manage to find and utilize as food in the wild. Therefore we will limit our study of the ecology of Drosophila to live yeast cultures, though recognising the importance of the axenic tests as a source of information on the physiology of growth of Drosophila.

Let us now turn a critical eye on the particular ecological conditions which face growing larvae of Drosophila in the three systems above mentione: virals, bottles and cages. We know that the effects of crowding are, in order of appearance: increase in development time, decrease in body size and decrease in viability (Forbes Robertson, 1959). In the absence of detectable behavioural effects on the growth of Drosophila we must conclude that the alterations in the parameters just mentioned are a consequence of food shortage. A postulate that follows from this conclusion is that any attempt to study the population genetics of Drosophila without paying due attention to ecological restrictions like this will be a waste of time. To our knowledge the levels of crowding usually adopted in vials and

and bottles are arbitrarily chosen and the rythm of pot substitution in the cages is determined more by convenience of management than by a serious consideration of Drosophila ecology.

One way of standardising feeding opportunities is by standardizing the quantity and quality of the food supplied to the larvae. It is easier to standardise the quality than the quantity and although in nature several species of yeast will be found, each with its own nutritive qualities (El-Helw and Ali, 1969) it is reasonable to choose one of them as a basis for our study. We chose Sacharomyces cerevisiae. The problem of quantity is trickier and more subtle: how much food should be given to the larvae to simulate natural conditions? It is the same as asking what are the selection pressures in nature. There is no uniform selection pressure in nature, since the feeding opportunities depend very much on the size and number of the niches available for colonization as well as on the population size of Drosophila and both factors vary with time.

One way of circling this difficulty is to establish a laboratory population in a cage and to run it for a few years. Provided we have a constant rythm of introduction of new pots in the cage we can say that after that time it is likely that the population has reached a certain genetic equilibrium and is adapted to the environment it has been experiencing even if this is not a completely natural one. We have got such a population - Pacific - kept in cage conditions for

about 8 years. Evidence that the population shows some degree of adaptedness comes from periodical measurements of body size, showing relative stability of the mean of this character. If we now perform a crowding test on this population, we'll be able to see which level of crowding gives a value for body size similar to the average value found in the cage over a certain interval of time (Fig. 1). This level of crowding will be used throughout all our competition experiments, independently of the genotypes competing and will be referred to as the "cage level" - 30 eggs/vial.

At the cage level (or the similar level of 40 eggs/vial) the reduction in viability is around 20 to 25% of the viability under optimal conditions, not a very marked decrease if we compare it with the estimate obtained by Kinross (1969) where only 10% of the eggs laid in a population cage reach adulthood. Body size varies accordingly to the day on which the individual hatches since it depends on the amount of food available during the post-critical period of growth and this varies with time, the average reduction below optimal oscillates between 35 and 40%. The parameter of fitness more substantially affected, however, is development time which is increased from its range of 8-9 days under optimal conditions to 9-15 days under competitive conditions.

We can now see that the optimal conditions under which selection experiments are carried out are not representative of the conditions usually met with by the larvae in the population cages. In this sense we need to establish the connection between the response to selection under optimal and under competitive conditions by selecting for body size under competitive conditions.

5. DESIGN OF EXPERIMENTS

A. Selection - Selection was carried out on body size and development time, both forwards and backwards.

Body size - Selection was usually done on flies grown under optimal conditions (sel 1, 2 and 4) although in one occasion competitive conditions were used (sel 3). The base population was always obtained by sampling the population cage.

When selection was carried out under optimal conditions 20 virgin ♀♀ and 20 ♂♂ were measured for thorax length from each of 5 cultures with an initial number of eggs of 70 per culture. The extreme 4 individuals of each type and sex were chosen as founder members of the large and small body size lines. In subsequent generations the 4 largest individuals of both sexes were selected in the large line and the 4 smallest in the small line. The selected flies were then allowed to mate at random in a bottle and to feed for a period of three days. Eggs were collected randomly and grown under optimal conditions to provide the individuals

for the next round of selection. When necessary, eggs were also utilized for competition tests according to the procedure already described.

For the experiment referred to as sel.3, ten cultures, with 30 eggs per culture (collected overnight), were set up. Virgin females and males were collected from the beginning to the end of hatching. All the individuals were measured, the extreme two individuals of each sex and culture being selected in each line. In each generation, eggs were cultured under competitive conditions to provide the next generation for selection and a "switch test" was conducted in which a sample of these eggs was cultured under optimal conditions for an assessment of the "real" body-size of the flies. After 4 rounds of selection a fixed-frequency competition test was run against the Pac white population. As in the case of selection under optimal conditions no attention was paid to development time since selection acted only after all the viable individuals had hatched.

Back-selection for body size followed exactly the procedure for selection under optimal conditions and was carried out only on the wild-type lines of sel. 4, until the unselected level was reached for both selected lines.

Controls for all these experiments were represented by all the individuals hatched in the control line, irrespective of their development time.

Development time - Selection for development time was performed on flies grown under competitive conditions at a crowding level of 30 eggs/vial (collected over a 2-hour period) with ten replicates per line - sel. 5. Flies were classified into 3 groups according to their development time: fast, medium and slow developing. In every generation the fastest flies in the fast line and the slowest in the slow line were chosen as parents of the next generation. The proportion of flies selected was not constant since it depended on a compromise between keeping a minimum population size (20 pairs per line) and the highest selection intensity.

A control was kept in which all the flies that hatched in the 10 control cultures were allowed to breed. Also, a "switch-test" to optimal conditions was performed every generation to assess the "real" body size of the selected flies.

After 4 generations of selection a competitive test (fixed frequency) against Pac white was done.

Back selection for development time was done on two sets of lines, selected for large and small body size and their controls, namely Sel 2 and Sel 4 (WT). In both the large and the small as well as in the controls, selection was always for fast development time. Switch tests to optimal conditions were carried out to judge any possible changes in body size.

B. Relaxation of selection - Selection for body size was relaxed at various stages in the different selection experiments: Sel 1 was relaxed at generations 4 and 9, sel. 2 was relaxed at generation 7 and sel. 4 (WT) was relaxed at generation 5.

Sel. 1 was relaxed under two types of conditions: at Gen.4 it was relaxed for both lines, under optimal and under mild competitive conditions (10 eggs/vial). Switch tests from competitive to optimal conditions were carried out in all of the 4 generations of relaxation to check for alterations in body size. At Gen.9 selection was relaxed for two generations, under a wide range of crowding conditions, followed by a switch test to optimal conditions; releaxation was also conducted under two other sets of competitive conditions, namely bottles and population cages with periodic tests under optimal to detect any change in body size. When bottles were used the flies were shaken from the old bottle into a new one after hatching had proceeded for a few days. The conditions in the cage were the same as those observed for every cage maintained during these experiments, i.e. a new pot was introduced regularly every second week.

Selection 2 and Sel. 4 were relaxed under optimal conditions.

C-Tails of the distribution Vs. the median - A competition experiment was performed to compare the competitive ability of the extreme individuals present in an unselected population with that of the

intermediate ones with respect to body size. For this purpose eggs were collected from a sample of individuals from the population cage and cultured under optimal conditions in 5 replicate cultures. All the individuals hatched were measured and 12 of each sex were selected per culture comprising the 4 from either extreme and the 4 closest to the mean value. Individuals within each of the 3 classes were allowed to mate freely. Eggs were collected and grown in competition (fixed-proportion) with a common competitor. This experiment which was replicated simultaneously on the Pac WT and the Pac white populations (using as a competitor the Pac white and Pac WT populations respectively) constituted the first generation of the Sel.4 experiment.

D. Competition

The experiments done to study competition followed this order:

1. Experiments designed to characterize the base population in this study as well as the marked sub population (Pac W).

   a) competition between these two populations under variable frequency conditions.

   b) competition between the two populations at fixed-frequency (1:1) but varying the time course.

2) Once the physiological difference between these two strains was reasonably well identified, this knowledge was used to suggest possible interpretations for the productivity patterns of lines selected for large and for small body size and also to make predictions as to the outcome of future competition between selected and unselected strains, based on these interpretations. The following competition experiments were carried out:

Selection for body size: (Fixed frequency) Sel 2 - Gen.2, 3,5. Sel 3 - Gen 4;

Sel 4 - Gen. 1 - 5 for the WT and for the W populations; Gen 4 - triple competition between WT and W selected lines and W^{ap} unselected population. Gen. 5 - variable proportion competition between large and small lines of different eye-type.

Backselection for size, sel.4 WT - fixed frequency competition after 2 generations of backselection.

Backselection for fast development times, sel. 2 and sel. 4 - fixed frequency competition after 4 generations.

Selection for development time - Sel.5 - Fixed frequency test at Gen. 4.

Procedure followed to study competition

Competition was always studied at cage level (40 eggs/vial) both with constant and variable frequency. The procedure followed was to collect eggs from both competitors (one of them marked with an eye mutation, usually PACIFIC White eye) simultaneously and over a period of two hours to minimize variance in the age of eggs and to culture them at 25°C in the competition vials. Usually, parallel cultures under OPTimal were kept to provide an estimate of the average potential size of the competing individuals. The parameters measured in a competition test were body size, daily productibity and development time of all the flies hatched in a culture.

6. STATISTICS

Analysis of variance

This was used for data with a single criterion of classification with or without equal replication for each group (STEEL and TORRIE,).

Source	SS_2	df	MS	
Between	$\Sigma \frac{Xi}{ri} - C$	t - 1	BSS/i-1	$F = \frac{MSB}{MSW}$
Within	TSS-BSS	$\Sigma ri - t$	WSS/Σri-i	
Total	$\Sigma_{ij} X^2_{ij} - C$	$\Sigma ri - 1$		

$$C = \frac{X^2}{\Sigma ri}$$

where i denotes the series of treatment, j the replicates within treatments, t the number of treatments and r the number of replicates in a treatment.

Whether or not the F test was significant, we felt justified in comparing the means two by two when the comparisons had been previously planned, e.g. selected lines vs. control or differences between selected lines. This was done by the use of a t-test with a denominator equal to:

$$sd = \sqrt{\frac{S_1^2}{n_1} + \frac{S_2^2}{n_2}}$$, with $n_1 + n_2 - 2$ degrees of freedom.

χ^2 analysis was done for competition tests only to check differences in viability. The χ^2 on totals for 5 replicates (degrees of freedom) was compared with the χ^2 for heterogeneity between replicates (number of replicates minus 1 degrees of freedom).

Competition index - Whenever the proportion at which two competitors existed was different from 1:1 a competition index was calculated to provide a relative indication of the differences in development time between the competing strains, since the difference between the numbers hatched each day could not be used on account of the different initial frequencies used.

The index is calculated as follows:

$$C.I. = \frac{\text{No. of adults hatched of genotype A}}{\text{Total no. of adults hatched of genotype A}} - \frac{\text{No. of adults hatched of genotype B}}{\text{Total no. of adults hatched of genotype B}}$$

This index is an indicator of the ability to grow under competitive conditions since it does not pay any attention to viability. Therefore, strains with widely different viabilities can have the same C.I. A test on differences in viability between the competitors is therefore required whenever this competitive index is used.

"Since the struggle for existence is chiefly a struggle for subsistence, a careful comparative account of the food of various competing species and genera at different places and seasons and at all ages of the individuals cannot fail to throw much light upon the details, causes and effects of the struggle."

FORBES (1925).

COMPETITION

a) THEORETICAL ILLUSTRATION

1. Relevant conditions: As we have seen, we must find conditions for a study of competition which are ecologically meaningful. We chose the competitive conditions described earlier and a level of crowding corresponding to that of population cages as the conditions for our experiments.

However, the ecological conditions chosen by different authors vary considerably. BARKER (1961), GALE (1964) and BARKER (1970 and others) used a dead yeast system consisting of a dead yeast suspension on an agar gel. Since there is little or no growth of the yeast population in these cultures, the food available to the larvae follows a continuously decreasing curve with time. When the volume of medium provided is relatively large compared with the volume of larvae feeding on it, it is likely that the concentration of the nutrients will remain little changed during the development of the larvae even though the absolute amount of food in the culture decreases progressively.

These conditions are desirable when performing experiments designed to study physiological changes, as the ones performed on the axenic media. Ideally it would be advantageous to have a volume of medium so large that recirculation of the medium through the digestive apparatus of the flies would be entirely avoided thus keeping the concentration of the nutrients constant. When the cultures are crowded, the concentration of nutrients in the food will decrease from its initial amount to the level reached when all individuals have stopped feeding. In this way, the dead yeast systems are different from the live yeast ones since in the latter, two feedback loops are operative, from predator to prey and vice versa, whereas in the former, the only prey to predator regulation effect exists. In other words, an oscillation of a given sign of one of the components of the system (predator to prey) determines an oscillation of the opposite sign in the other component. In the dead yeast system, the prey component can vary in only one direction - downwards!

The consequences of these differences between the two systems (live and dead yeast) are reflected in several parameters of fitness, namely body size, viability and development time.

Body size is, as we have seen, a consequence of the amount of food available during the post critical period. Since the concentration of food in a dead yeast system decreases progressively, the later larvae reach the critical stage later have a smaller body size. Flies grown in live yeast systems may exhibit a quite different pattern for body size due to the regeneration of the yeast population.

Development time will exhibit a much smaller variance in the dead than in the live yeast systems. In live yeast systems the larvae exhibit a "waiting" behaviour, i.e. they are able to increase their development time considerably until more favourable conditions appear. This will not be possible in dead yeast systems because the food available will not be sufficient for the maintenance of the growing individuals. Death will ensue for all but the fastest developing individuals. For this reason, when comparing results from LYS and DYS, the flies hatching early in LYS should be equated to all the flies hatching in DYS. In other words whereas in LYS the slow-developing flies are able to "wait" until the fast developing flies have completed their development and the intensity of competition is lowered, in the DYS the flies are not able to "wait" since there is nothing to wait for because there is no regeneration of the yeast population as happens in LYS. Therefore viability will be lower in DYS than in LYS.

For the reasons stated and because our knowledge of Drosophila's ecology is limited we think that live yeast systems are to be preferred to dead yeast ones for competition studies. Another reason for this preference is that LYS provides a better estimate of the variance in development time and also allows us to make inference about the physiological basis of competitive ability through the comparisons of body size between competitors with the same development time.

2. Criteria for competition: There are two different conceptual approaches to the study of competition. The first which is used by almost all students of competition refers to the results of competition between two or more populations or genotypes. In this approach, only the results of competition are important, therefore no predictions can be made as to the results of future competion between any two other strains even when they are related to the original ones (AYALA, 1969, 1970, 1971; BARKER and PODGER, 1970). Typical statements from people who endorse this type of attitude are: "the Gause principle doesn't hold" or "there is frequency dependant selection". Alternatively we find workers interested in identifying the causal components of competition since this would allow predictions to be made in relation to any competitive situation where thes components are known (BARKER, 1961). This is the attitude adopted by us in our studies of competition.

As to the type of problem studied it is logical that problems of genetic equilibria within populations should be studied with the help of intraspecific competition, since these represent the conditions under which these equilibria will or will not be attained. The use of interspecies competition in the study of these problems (BARKER, 1962, 1966) does nothing but add to the number of unknowns in the problem.

DIAGRAM no. 1 - DETERMINATION OF BODY SIZE

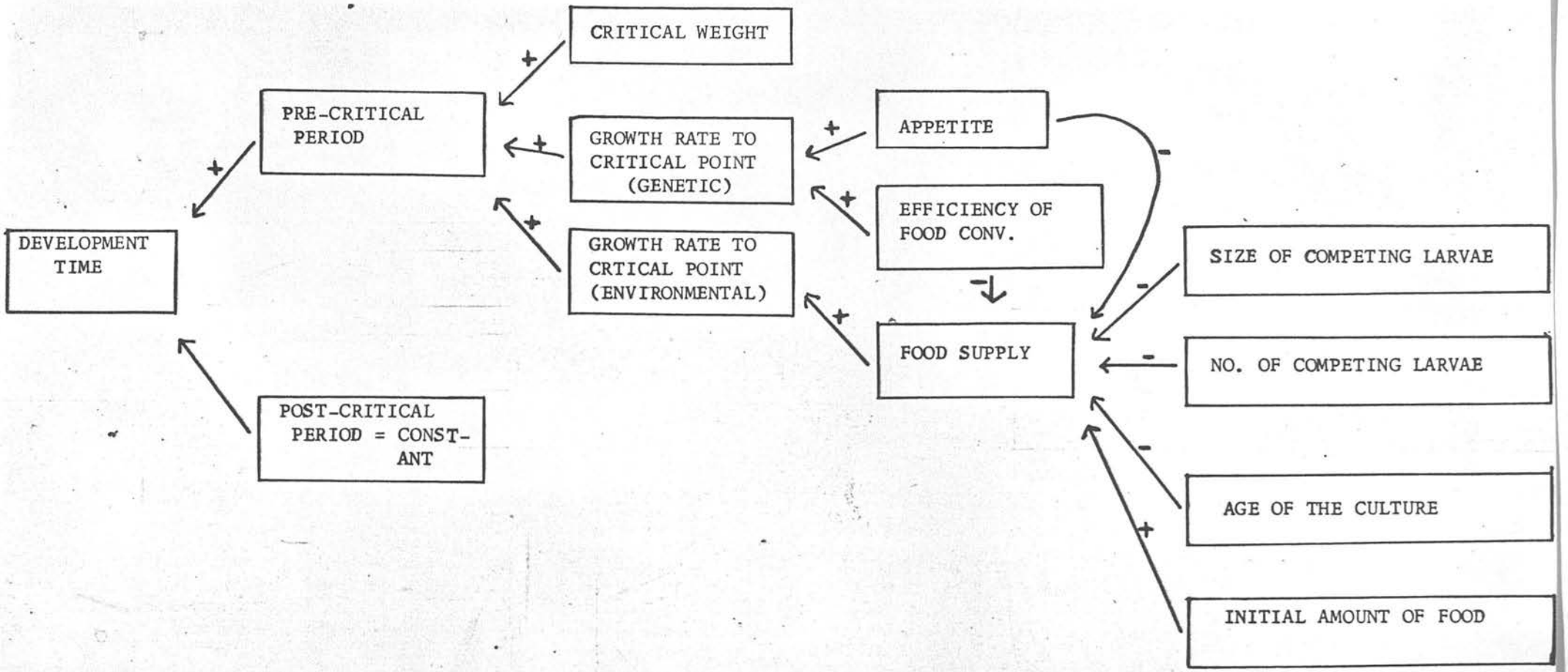
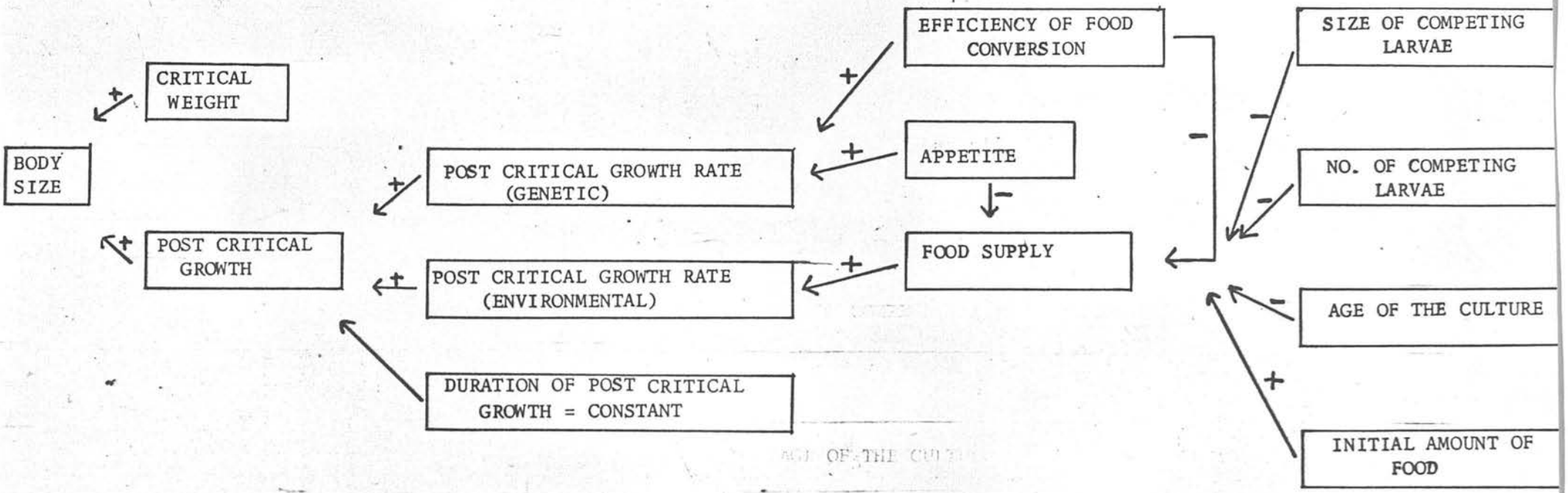


DIAGRAM no. 2 - DETERMINATION OF DEVELOPMENT TIME



If we now turn to the way competition is measured we can see clearly two types of experimental design. The first one concerns experiments where one or more characters are measured and interpreted individually. The second is the analysis of a system represented by the inter-relations of four characters: body size, development time, daily productivity and viability. Diagrams for development time and body size are shown in Figures annexed.

The assumptions underlying the interpretation of competition data are:

a) The differences in the speed of growth must have a genetical component when we eliminate the variance in the age of the eggs. Fitness will be negatively correlated with development time.

b) The phenotypic body size of the flies hatching from a competitive system is a consequence of the genetic body size but principally of the amount of food available during post-critical growth.

c) As a consequence of the previous paragraph, flies with the same development time must have the same body size if the physiological mechanisms underlying growth are uniform. Failure to verify this assumption implies that the same duration of development can be achieved through different physiological pathways.

d) These differences are likely to be exhibited in a predator-prey system as indicated before.

3. The theory of competition: As we noted above, the ecology of a competitive situation is basically a problem of population dynamics of the predator-prey type of relationship, the predator being the larval population and the prey the yeast population. In our case the abundance of the predator (or biomass) is limited by the abundance of prey, i.e. the number of prey taken by each predator decreases as the abundance of the prey decreases. In other words there is a regulating influence of the prey on the predator (we will follow closely the methodology of MAYNARD-SMITH, 1968). Other assumptions are that each predator eats a number of prey proportional to the abundance of the prey (concentration of yeast cells in the medium), that the prey is distributed homogeneously throughout the medium and that there is no competition for space between larvae (no territorial division). It is also assumed that the efficiency of food conversion into biomass (or potential offspring if we bear in mind the correlation between body size and egg production found by FORBES ROBERTSON, 1957) is constant, i.e. independent of age and food input.

If Xn and Yn represent the biomass of prey and predator respectively, at time n and R and r represent the maximum growth rates of the prey and the predator respectively, the number of prey eaten by each predator will be CXn (C being the feeding rate) and the biomass produced by each predator will be equal to

$$\text{Constant} \cdot CXn = kXn \quad \text{and}$$
$$Yn+1 = kXnYn$$

It can be shown that

$$Xn+1 = RXn-(R-1)Xn^2-(R-1)Xn^2/XE-CXnYn \quad \text{and}$$

$$Yn+1 = rXnYn/XE$$

where XE is the density limit of the prey population in the absence of predators.

Let us suppose (MAYNARD-SMITH, op cit.) that the prey are at their equilibrium density XE in the absence of predators and that a few predators are then introduced. We will make R=1.5 (in which case the prey population would approach XE without oscillation) and XE = 100. Let us further assume that when Xn=XE each predator kills (eats) 50 prey, therefore CXE = 50 or C = 0.5. Also assume that this diet is sufficient to enable the predator to double its biomass every time unit, therefore r = 2.

We are now able to iterate the equations above. We will start with the prey at the equilibrium density and a relatively rare predator (say, Y1 = 0.2) and we will look at the effects of varying C (the feeding rate or appetite) and its correlate, r, on the food availability (in absolute terms) and in the productivity of the predator and on the equilibrium values of Xn and Yn. Because one of our assumptions is that the biomass produced by each predator is proportional to C, r will have to be calculated for each value of C on the basis of a given direct correspondence between C and r. This assumption may not be true for all values of Xn since it is conceivable that above a certain level of food imput (quality of food)

differences in C and r will not be reflected in the productivity parameters under optimal conditions; but since this is not a competitive situation by definition we will not bother with it. The product C.r at a given time represents the growth rate at that time.

EQUILIBRIUM VALUES OF PREY AND PREDATOR

C	r	X_n	Y_n
0.5	2.0	50.00	0.5
0.48	1.92	52.08	0.48
0.40	1.60	62.50	0.38

The analysis of the table reveals that as C and r decrease, Xn increases; in other words there will be more food available but there will be less biomass at equilibrium as C decreases but more food available to any "foreign individual" capable of utilizing it. If numbers are kept at the expense of size we will see a reduction in average body size but not reduction in viability otherwise size will be kept constant but the viability will be reduced. However, since our Drosophila system shows some discontinuity (due to pupation) it is possible that equilibrium values are not so important in this context.

Having considered a model for competition based on physiological parameters like C (appetite), r(efficiency of food conversion) and critical size we will proceed to look at the conditions under which the system can be simulated in a computer.

Restrictions of the simulation

1. The model is a deterministic one, therefore no variances are involved, only the means; this fact has two consequences:

   a) We do not know the characteristics of the distribution involved (magnitude of standard deviation, skewness, curtosis etc.) thereby giving us no idea about the degree of overlapping of the populations. Within populations we do not know how biomass is distributed between the competing individuals.

   b) The predictions made will not adequately cover competition between small numbers of individuals, due to the sampling effects involved.

2. We know little about the liability to death of the different stages of Drosophila; we also do not know how long the larvae are able to "wait" for better conditions without dying. We would also welcome information on how efficiency varies with food imput or how critical size varies with time.

3. The third restriction which we already considered is the non-introduction of the duration of the 2nd period as a parameter in competition. Indeed we will be using larval size at pupation as an indication of critical size. This assumption may well prove to be untrue whenever we are not dealing with competition between individuals from the same population.

We shall begin by examining the effects of crowding on strains which differ in certain physiological characters. We shall then study competition at a fixed level of crowding but at variable frequency between these strains.

CROWDING

The examination of the table/reveals:

1) Crowding affects different components of fitness in different ways. The first to be affected is development time which is positively correlated with intensity of crowding as long as all the individuals complete their development, i.e. as long as long as R biomass at t max is 1.00. From this point onwards an increase in intensity of crowding will leave development time unchanged but realized biomass will be affected, i.e. decreased. This could mean either a reduction in size or a reduction in viability, since, as explained before the measure of critical size used here is size at pupation time which we assumed to be correlated with critical size, under the conditions studied. In any case a reduction in R biomass will undoubtedly mean a reduction in the average reproductive potential of the individuals concerned.

2) Strains which differ in feeding rate, but which are similar in other respects will always exhibit a superiority of the fast feeding one over the other, as long as R biomass = 1, i.e. all the individuals can complete their development. This superiority will be reflected in a shorter development time. However, when R biomass decreases from 1 towards zero, as crowding increases, this superiority fades away and becomes zero at the highest level of crowding (1.000). One point we must make at this stage is that the differences in development time between the two strains when R biomass = 1 may or may not be detected if we look at the development time to the adults state of Drosophila, due to the circadian variation in hatching; in other words a difference in development time smaller than a certain minimum should be examined in terms of the development time of the larvae rather than that of adults.

We can easily see how strains which differ in development time but not in viability under relatively unrestricted conditions (R biomass = 1) can nevertheless exhibit similar development times and viabilities when grown under restricted conditions (R biomass < 1). This is possible when the difference between strains is caused by differences in feeding rate and is not possible when the difference is in terms of efficiency of food conversion.

3) Another point worth mentioning here is the fact that in all pure cultures, provided the growth parameters fall within certain limits (MAYNARD-SMITH, 1968) as they do here, the oscillations of the predator

(biomass) are "damped", i.e. their amplitude decreases progressively. The relevance of this point will be fully appreciated when discussing between strain competition.

We have looked at the effects of crowding on two strains of Drosophila which differ in feeding rate but have the same efficiency of food conversion and critical size. We will now turn to the effects of competition between strains, which differ in some growth parameters on the competitive index measured as a difference between their realised productivities and on overall productivity (biomass produced per culture).

VARIANCE OF THE AGE OF THE COMPETING INDIVIDUALS

Let us consider the effects of variation in the age structure of the competitors, both in cultures with competitiors with identical physiological characteristics and in cultures where competitors differ in their feeding rate.

We can see from Table No 2 that

a) Variance in age increases the total productivity of the cultures. This is true both for situations where the distributions of age overlap partially (±2 and ±4) and for situations where little or no overlapping occurs (±8). Provided the distributions overlap partially the larger the variance the greater will be the biomass produced at a given time (say t = 8).

b) When the distributions of age overlap to some extent the variance in age is positively correlated with the competitive index as well as with productivity at a given time say t = 8. If the distributions overlap slightly or not at all then the time at which the older competitor reaches a 100% level in realized biomass (t Max.) and the difference between this value and the corresponding one for the younger competitors are both a function of the differences in feeding rate between the two competitors: the larger this difference the earlier will the older competitor complete its development and the later will the younger one do the same.

c) The competitive index also varies proportionally with the differences in feeding rate and inversely with productivity at the time when the maximum biomass is reached for y.

d) When the faster feeding competitor is handicapped (C1 = 0.48, C2 = 0.50) its advantage is reduced but still positive for t - 2 and t - 4.

COMPETITION UNDER VARIABLE FREQUENCY

We have simulated competition with variable proportions of the strains which differ in either of these parameters:

a) Feeding rate

b) Efficiency of food conversion

c) Critical size.

The results, presented in the adjoining tables can be summarized as follows:

1. When strains exhibit a small difference in feeding rate (C1 = 0.50, C2 = 0.48) C.I. is negatively correlated with the percentage of the fast-feeding competitor. There is also a decrease in the realized biomass of both competitors. Productivity varies little although showing a maximum when the competitors are present in equal quantity.

When C1-C2 is larger the same pattern is observed but the differences are more marked. Also the development time of the fast developing competitor is positively correlated with its frequency.

2. When the strains have the same feeding rate (R1 = C1 X 4; R2 = C2 X 36) but differ in the efficiency of food conversion, the competitive index is positively correlated with the frequency of the more efficient competitor up to 0.25 and negatively correlated thereafter. Productivity is positively correlated with the frequency of this competitor as well as development time, at least at the 0.125 and 0.25 frequencies. Both competitors have their biomass progressively reduced as the frequency of the more efficient one increases.

The 2nd row of values quoted for the frequencies of 0.375 and 0.500 refer to the peak following the zone reached at t = g. At the time referred (t = 20.23 and t = 21.33 respectively) the two competitors exhibit much higher C.I. than at t = g thus showing that the difference between them tends to expand (divergent oscillations) even when the total biomass (PRD) is "damped", i.e. tends to its equilibrium value.

3. When the strains have the same feeding rate and the same efficiency of food conversion but differ in critical size (Table No. 6) both the competitive index and productivity are constant with variable frequency of the competitors.

We now see how changes in the three parameters of growth studied here, feeding rate, efficiency of food conversion and critical size affect measurable parameters like biomass and development time. Ideally we would like to split biomass into its body size and the number of individuals hatched (productivity). However, this will not be possible before we have information concerning the variance of body size in the culture, in other words we need to know how the biomass is distributed between the individuals in a culture. When we acquire this information we will be able to use a non-deterministic model to simulate competition which would take into account the variance in body size of the growing individuals.

In any case with or without the knowledge of the variance of larval body size, we have a system which enables us to analyse growth and body size as the result of interactions of physiological parameters with the environment and not through the independent study of its parameters.

Our computer simulation represents a reasonable approximation to the natural (live yeast) situation. Certainly some improvement will be

TABLE No.1

SIMULATION OF CROWDING

LEVEL OF CROWDING	C = 0.48 R = C x 4		C = 0.50 R = C x 4		C = 0.50 R = C x 3.6	
	t max	R biomass	t max	R biomass	t max	R biomass
0.125	6.84	1.00	6.42	1.00	1.55	1.00
0.250	7.05	1.00	6.65	1.00	7.93	1.00
0.375	7.37	1.00	6.96	1.00	8.37	1.00
0.500	7.75	1.00	7.31	1.00	9.03	1.00
0.625	8.53	1.00	7.85	1.00	10.00	0.89
0.750	9.00	0.88	9.00	0.92	10.00	0.72
0.875	9.00	0.73	9.00	0.74	10.00	0.59
1.000	9.00	0.62	9.00	0.62	10.00	0.50

t max is the time at which maximum biomass is achieved; R biomass is realized biomass or the ratio between the actual biomass and the biomass required to allow all the individuals to complete development; C stands for feeding rate; R stands for growth rate; R/C = efficiency of food conversion.

SIMULATION OF COMPETITION VARYING THE AGE STRUCTURE OF THE COMPETITORS

TABLE No.2

C1 = C2 = 0.50

T - 8

T	Y	Z	Ry	Rz	C.I.	PRD
8.3	0.684	0.100	1.000	0.141	0.543	0.784
13.28	0.000	0.684	0.000	1.000	-1.000	0.684
AC 13.28	0.684	0.684			0.000	1.368

T-4

T	Y	Z	Ry	Rz	C.I.	PRD
8	0.507	0.422	0.741	0.617	0.123	0.929

T-2

T	Y	Z	Ry	Rz	C.I.	PRD
8	0.428	0.428	0.627	0.627	0.000	0.857

C1 = 0.50
C2 = 0.48

t - 8

T	Y	Z	RY	Rz	C.I.	PRD
7.45	0.684	0.000	1.000	0.000	1.000	0.684
13.77	0.000	0.684	0.000	1.000	-1.000	0.684
AC 13.77	0.684	0.684			0.000	1.368

t - 4

T	Y	Z	Ry	Rz	C.I.	PRD
8.00	0.536	0.364	0.784	0.532	0.251	0.900

t -2

T	Y	Z	Ry	Rz	C.I.	PRD
9.00	0.497	0.358	0.726	0.524	0.202	0.855

C1 = 0.48
C2 = 0.50

t - 8

T	Y	Z	Ry	Rz	C.I.	PRD
7.79	0.684	0.000	1.000	0.000	1.000	0.684
12.55	0.000	0.684	0.000	1.000	-1.000	0.684
AC 12.55	0.684	0.684			0.000	1.368

t- 4

T	Y	Z	Ry	Rz	C.I.	PRD
8.00	0.428	0.474	0.626	0.693	-0.067	0.902

t -2

T	Y	Z	Ry	Rz	C.I.	PRD
9.00	0.358	0.497	0.524	0.726	-0.202	0.855

TABLE No.3.

COMPETITION-FREQUENCY DEPENDANCE : $C_1 = 0.50$ $R_1 = C_1 \times 4$

SMALL DIFFERENCES IN FEEDING RATE: $C_2 = 0.48$ $R_2 = C_2 \times 4$

$CS_1 = CS_2$

Frequency of Y	T	Y	Z	Ry	Rz	C.I.	PRD
$Y_1 = 0.125$	9.00	0.140	0.709	0.821	0.592	0.229	0.850
	20.65	0.171	0.537	1.000	0.448	0.552	0.708
$Y_1 = 0.250$	9.00	0.269	0.583	0.788	0.568	0.220	0.853
	21.50	0.342	0.444	1.000	0.432	0.568	0.786
$Y_1 = 0.375$	9.00	0.388	0.466	0.756	0.545	0.211	0.855
$Y_1 = 0.500$	9.00	0.497	0.358	0.726	0.523	0.203	0.855
$Y_2 = 0.625$	9.00	0.597	0.258	0.698	0.503	0.195	0.855
$Y_1 = 0.750$	9.00	0.688	0.165	0.671	0.483	0.188	0.854
$Y_1 = 0.875$	9.00	0.772	0.079	0.645	0.463	0.181	0.852

TABLE No.4

COMPETITION - FREQUENCY DEPENDANCE : $C_1 = 0.50$ $R_1 = C_1 \times 4$

LARGE DIFFERENCES IN FEEDING RATE : $C_2 = 0.40$ $R_2 = C_2 \times 4$

CS1 = CS2

Frequency of Y	T	Y	Z	R_y	Rz	C.I.	PRD
	7.42	0.171	0.280	1.000	0.234	0.766	0.451
Y = 0.125	14.00	0.000	0.596	0.000	0.498	-0.498	0.596
	Ac 14.00	0.171	0.596	1.000	0.498	+0.502	0.767
	7.64	0.342	0.229	1.000	0.223	0.777	0.571
Y = 0.250	15.00	0.000	0.612	0.000	0.596	-0.596	0.612
	Ac 15.00	0.342	0.612	1.000	0.596	+0.404	0.954
	7.93	0.513	0.181	1.000	0.211	0.789	0.684
Y = 0.375	17.00	0.000	0.651	0.000	0.761	-0.761	0.651
	Ac 17.00	0.513	0.651	1.000	0.761	+0.239	1.164
	8.43	0.684	0.129	1.000	0.188	0.812	0.813
Y = 0.500	19.53	0.000	0.684	0.000	1.000	-1.000	0.684
	Ac 19.53	0.684	0.684	1.000	1.000	0.000	1.368
Y = 0.625	9.00	0.809	0.081	0.946	0.158	0.788	0.891
Y = 0.750	9.00	0.838	0.046	0.817	0.136	0.680	0.885
Y = 0.875	9.00	0.850	0.020	0.710	0.118	0.591	0.870

TABLE No.5.

COMPETITION-FREQUENCY DEPENDANCE: $C_1 = 0.50$ $R_1 = C_1 \times 4$

DIFFERENCES IN THE EFFICIENCY OF FOOD CONVERSION $C_2 = 0.50$ $R_2 = C_2 \times 3.6$

CS1 = CS2

	T	Y	Z	Ry	Rz	C.I.	PRD
Frequency of Y							
$Y_1 = 0.125$	8.70	0.171	0.529	1.000	0.442	0.557	0.700
$Y_1 = 0.250$	9.80	0.342	0.405	1.000	0.395	0.604	0.747
$Y_1 = 0.375$	9.00	0.464	0.333	0.904	0.389	0.515	0.797
	20.23	0.513	0.113	1.000	0.131	0.869	0.626
$Y_1 = 0.500$	9.00	0.572	0.246	0.837	0.360	0.477	0.819
	21.33	0.684	0.080	1.000	0.117	0.883	0.764
$Y_1 = 0.625$	9.00	0.663	0.171	0.775	0.333	0.442	0.834
$Y_1 = 0.750$	9.00	0.738	0.105	0.719	0.309	0.410	0.844
$Y_1 = 0.875$	9.00	0.799	0.491	0.668	0.286	0.381	0.848

TABLE No.6

COMPETITION WITH VARIABLE FREQUENCY OF STRAINS DIFFERING ONLY IN CRITICAL SIZE

$C_1 = C_2 = 0.50$ $R_1 = R_2 = C \times 4$ CS1 = 0.684 CS2 = 0.750

Frequency	Tmax	Y	Z	Ry	Rz	C.I.	PRD
0.25	8.00	0.214	0.643	0.627	0.571	+0.055	0.857
0.50	8.00	0.428	0.428	0.627	0.571	+0.055	0.857
0.75	8.00	0.643	0.214	0.627	0.571	+0.055	0.857

possible in the future through the use of better programs and the accurate fitting of physiological constants whenever they are known. Nevertheless given some reasonable inferences about the differences in the physiology of any two competitiors our competition system will enable us to have a reasonable approximation to their behaviour in competition.

We shall exemplify what was said, by considering the outcome of competition between the Pac WT and the Pac W population when their frequencies vary. We shall also study the effects of varying the time course of the two competitors.

The results of these experiments are represented in Tables 7 and 8.

A. VARIABLE PROPORTION EXPERIMENTS

(i) The differences in body size between the two strains within days never differ from zero.

(ii) The differences in development time expressed by the C.I. vary with the frequency of the comeptitors and the day in which these differences are measured. The correlation between the frequency of the WT strain and the competitive index is indicated on each day for one of the experiments (Table 8). The regression coefficient of the competitive index on frequency is also indicated.

(iii) Although the WT strain is always superior to the white one, the magnitude of this superiority is a function of its frequency. In the 1st day the correlation is highly positive meaning that the lower the frequency of WT individuals the greater the difference between WT and W. These differences in C.I. can be a consequence of a reduced

total productivity or the effect of changes in some physiological parameter like feeding rate or the efficiency of food conversion. Since the total productivity varies little between proportions we are left with the choice between feeding rate and the efficiency of food conversion. The latter involves a positive correlation between the frequency of the stronger competitor and early productivity; this is not observed therefore we must conclude that the difference in competitive ability between the 2 Pacific populations is caused, at least partially by a difference in feeding rate. We will conclude then that the effect of introducing the white gene into the Pacific background reduced the average feeding rate, but did not interfere with the process of growth otherwise since body size of the two populations does not differ (under optimal or competitive conditions). The development time measured under optimal as well as under suboptimal (pure culture) conditions is the same. We saw how our simulation of results of crowding explained this apparent contradiction. It is only when the two populations are mixed that the difference in competitive ability is exhibited. In this way it is not possible to predict the outcome of competition between strains differing in such a minor way as the ones considered here.

(iv) We can see that frequency-dependent selection is present in competition between the two Pacific populations, the fitness of the WT population increasing, as its frequency decreases. Provided we

know the magnitude the difference in feeding rate between the two populations we will be able to predict with exactitude the fate of the white gene when in competition with its wild-type allele or any other allele whose biological effects are known. In this way the results described differ from the ones presented by other workers on this subject.

B. VARIATION IN THE TIME COURSE

The experimental plan followed gave the white population a handicap in time of 2,4,6,12 and 24 hrs. - designated as A,B,C,D and E. The wild-type was handicapped in time by the same periods and the cultures were designated as G,H,I,J and L. A control was set up in which the age of the two competitors was similar; these cultures are referred to as F.

(i) The results indicate that the total number of individual produced in the different cultures does not vary substantially if we except the cases of the C and E cultures; since D has a total productivity which does not differ from the average we will assume that the result of C is an artefact.

(ii) In spite of this constancy in total productivity there is a large variation in productivity within days which corresponds to the initial handicaps. The productivity in the first 2 days is positively

correlated with the variance in the age of the individuals. This fact fits the predictions made by the results of our computer simulation.

(iii) The competitive index is also correlated with the initial variance in the age of the eggs. However when we compare the competitive index of (for the first 2 days) the cultures where the white population is handicapped with that of the cultures where the wild-type is handicapped we can see that the absolute value of the former is greater than that of the latter. This fact fits well the predictions made by the results of our computer simulation.

(iv) The results also indicate that a given initial difference in development time is "amplified" many times in the course of competition, suggesting that our model of competition is built on the right assumptions.

(v) The body size of the two competitors did not differ when measured under competitive conditions (within days).

Now that we have identified the probable cause of the differences between the Pac WT and white populations, we shall turn our attention to the study of the causes of the differences in body size which are consequent to selection and the way in which these differences can affect the fitness of the selected lines in competition with the unselected.

We shall also consider the evidence obtained by some authors on the results of competition between different species and the way in which these differences can be explained by our model competition.

TABLE 7

COMPETITION UNDER VARIABLE PROPORTION BETWEEN Pac WT and Pac White

Day	1		2		3		4						
Proportion WT/W	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	TOTAL PRD	% WT	% W	TOTALS	2 HET.
40/0		4.4		13.5		6.7		2.9	27.5				
30/10	+0.063	2.5	+0.011	14.4	-0.028	7.3	-0.042	3.0	27.2	74	26	0.08	2.07
20/20	+0.098	4.6	-0.023	14.7	-0.037	6.8	-0.020	1.4	26.5	51	49	0.18	4.70
10/30	+0.116*	2.2	+0.128*	13.5	-0.169**	9.7	-0.056	4.6	30.0	24	76	0.28	2.60
0/40		3.6		16.1		8.8		1.7	30.2				

F RATIo

C.I. COMPETITIVE INDEX
PRD - Productivity
The C.I. are tested for their difference from zero.

TABLE 8 : COMPETITION BETWEEN PAC WT and PAC W - VARIABLE PROPORTION

DAY	1		2		3		4		5		6		1+2					
PROP. WT/W	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	TOTAL PRD	% WT	% W	2 TOTALS HET.
40/0		0.9		8.5		9.7		2.7		1.2		0.6		9.4	23.6			
30/10	+0.058	0.3	+0.067	6.5	+0.065	13.6	-0.114*	4.3	-0.018	1.6	+0.011	1.4	+0.085	6.8	27.4	74	26	0.12 3.04
25/15	+0.088	0.4	+0.217**	9.3	-0.114	9.4	-0.09*	3.6	-0.002	2.0	-0.009	0.7	+0.244	9.7	25.6	60	40	0.48 3.19
20/20	+0.077*	0.2	+0.103	6.7	-0.049	10.6	-0.117	5.8	+0.031	0.8	+0.012	0.9	+0.124	6.9	24.7	46	54	1.46 7.50
15/25	+0.094*	1.30	+0.163**	7.0	-0.154	12.5	-0.05	3.0	-0.007	1.4	+0.001	0.5	+0.252	8.3	26.5	39	61	0.21 7.23
10/30	+0.184*	0.7	+0.138*	9.6	-0.229***	10.8	-0.067*	3.1	+0.044	1.4	+0.083	0.6	+0.207	10.3	26.2	26	74	0.04 2.36
0/40		0.9		9.1		8.2		2.6		1.2		0.6			22.6			
F RATIO																		
Correlation Proportion/ C.I.	-0.84*		-0.24		+0.89**		-0.72*		-0.71				-0.54					
REGRESSION PROP/C.I.	-0.21±0.07*		-0.07±0.16		+0.50±0.14*		-0.10±0.06		-0.09±0.05				-0.20±0.18					

C.I. = Competitive Index of WT in relation to W. PRD = Productivity. The C.I.'s are tested for their difference from zero.

TABLE NO.9 COMPETITION BETWEEN Pac WT and W VARIATION IN TIME COURSE

DAY	1		2		3		4		5		6		7		8		%		TOTAL
	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	WT	W	PRD
A	+0.4	0.4	+1.6	2.0	+0.4	9.2	-1.4	7.4	-3.6	4.4	-1.4	1.4	-0.2	0.2		0.0	42	58	25.0
B	+0.2	0.2	+1.8	1.8	+0.8	9.2	-3.6	7.2	-2.4	3.2	-0.8	1.2	-0.6	0.2	-0.2	0.2	40	60	23.6
C	+0.2	0.2	+2.4	2.8	-0.6	5.4	-3.6	4.8	-2.8	3.2	-1.2	1.6	-0.2	0.6	-0.4	0.4	33	67	19.0
D	+0.6	0.6	+4.0	4.0	+3.2	3.2	+0.2	2.2	-4.2	5.4	-3.8	3.8	-2.4	2.4	-0.6	1.0	43	57	22.6
E	+2.2	2.2	+5.4	5.4	+1.8	1.8	-0.2	0.2		0.0	-3.2	3.2	-4.8	4.8	-1.0	1.0	48	52	17.6
F	+0.2	0.2	0.0	1.2	+0.4	6.8	-2.2	6.6	-2.0	4.4	-0.8	1.2	-0.4	0.8	+0.2	0.2	39	61	21.4
G	+0.2	0.2	-1.0	1.4	+0.4	6.4	-1.2	7.2	0.0	5.2	-0.6	1.0	+0.2	0.6	0 .0	0.0	46	54	22.0
H	+0.4	0.4	+0.2	0.4	-1.0	5.8	-0.6	7.0	-1.0	5.8	+0.4	1.6	0.0	0.8	+0.2	0.2	47	53	22.0
I		0.0	-1.2	2.0	-4.8	7.2	-0.8	6.4	2.0	2.8	+0.6	2.2	+0.6	0.6	+0.6	0.6	43	57	21.8
J		0.0	-0.6	0.6	-5.0	5.0	-3.4	4.6	1.2	3.6	+2.0	4.4	+3.4	3.8	+0.4	1.2	35	64	24.2
L	-1.4	1.4	-7.6	7.6	-3.0	3.0	-1.2	1.2	+0.6	1.0	+3.2	3.2	+2.4	2.4	+2.4	2.4	39	61	22.2

SUMMARY OF SELECTION EXPERIMENTS

Expt. No.	Character Selected	Conditions	Relaxation Gen.	Relaxation Conditions	Back Selection Gen.	Back Selection Conditions	Development Time Gen.	Development Time Conditions
1	LARGE/SMALL BS	OPT	4	EXPT. 1 EXPT. 2	-	-	-	-
			9	EXPT. 1 EXPT. 2 EXPT. 3	-	-	-	-
2	LARGE/SMALL BS	OPT	7	OPT	-	-	7 (Relax)	CT
3	LARGE/SMALL BS	CT	-	-	-	-	-	-
4(WT)	LARGE/SMALL BS	OPT	5	OPT	5	OPT	5	CT
4(W)	LARGE/SMALL BS	OPT	-	-	-	-	-	-
5	FAST/SLOW DEVELOPMENT	CT	-	-	-	-	-	-

SELECTION EXPERIMENTS - BODY SIZE

RESULTS

A - BODY SIZE

(i) In all the selection experiments selection had an immediate response in both directions (see Fig 2 for Sel 1 and measurements under optimal for other experiments - table 9A).

(ii) In the selection 3 experiment, the response measured under sub-optimal conditions was more reduced than when selection was carried under optimal conditions. This is probably a direct consequence if the fact that this experiment was carried out under competitive conditions where body size is very much a function of the food available during the post-critical period and consequently the environmental component of the phenotypic variance will be inflated (table 15).

(iii) The differences in body size between selected and unselected were exhibited both under optimal and under competitive conditions (tables 9A, 10-18).

(iv) The two control populations (pac WT and Pac W) do not differ in body size measured under optimal and under competitive condition (within days, between strains comparisons - see tables indicated in iii).

B - COMPETITIVE ABILITY

(i) The competitive ability (Day 1 + 2) of all the selected lines in the early generations of selection decreased, with the exception of the white large line (sel.4) which increased its competitive ability in the first 2 generations of selection but reduced it thereafter (tables 9B/C). This reduction in competitive ability seemed to disappear after the 3rd

FIG-2

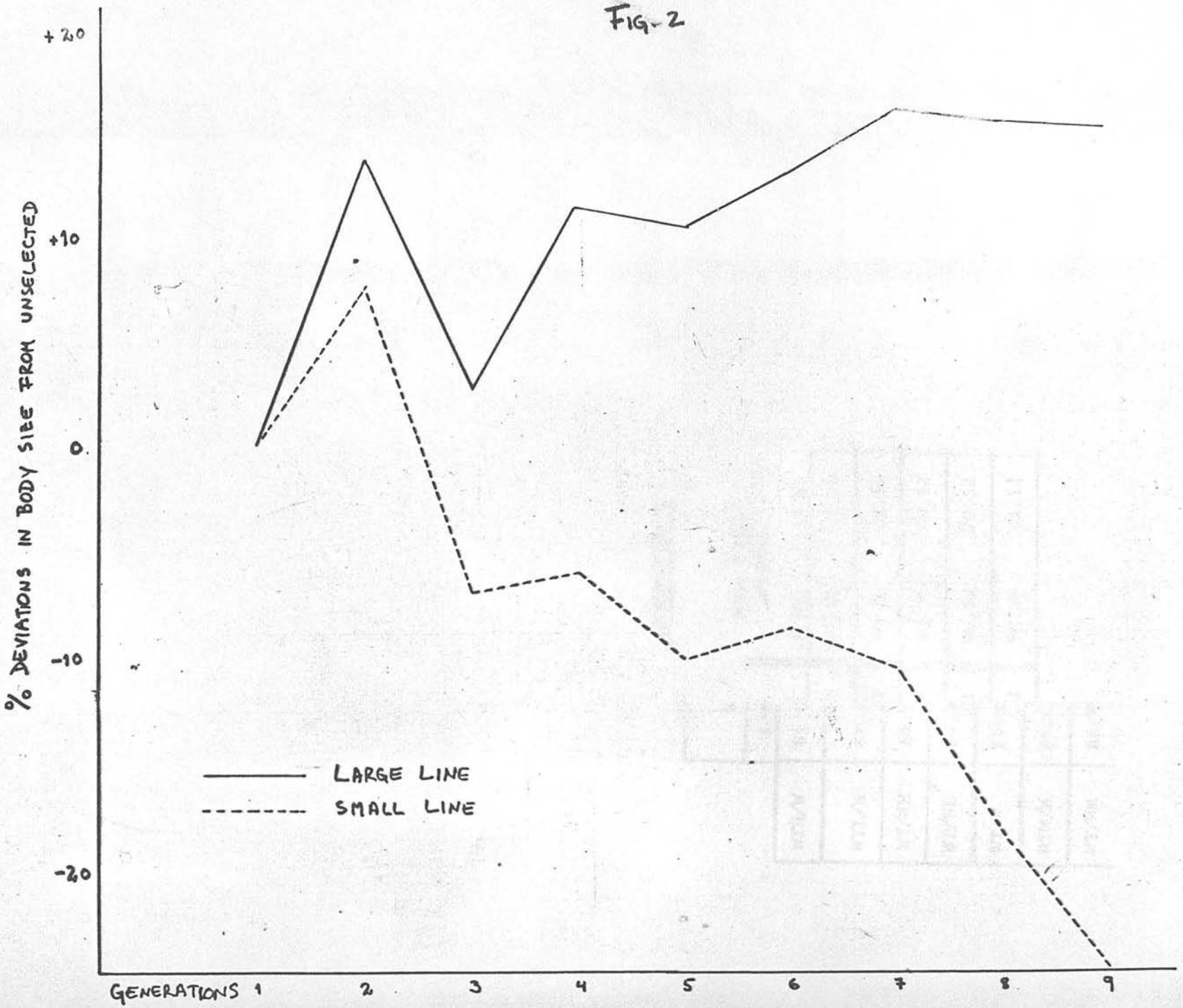

+20
+10
0
-10
-20
% DEVIATIONS IN BODY SIZE FROM UNSELECTED
LARGE LINE
SMALL LINE
GENERATIONS 1 2 3 4 5 6 7 8 9

TABLE 9 A BODY SIZE MEASURED UNDER OPTIMAL CONDITIONS

SELECTION 2

GENERATION 2

	BODY SIZE-OPTIMAL			
	♀ WT	♀ W	♂ WT	♂ W
LOW/W	88.75	93.22	48.40	55.40
HIGH/W	103.20	93.22	56.70	55.40
CO/W	99.42	93.22	59.47	55.40

GENERATION 5

	BODY SIZE-OPTIMAL			
	♀ WT	♀ W	♂ WT	♂ W
LOW/W	80.37	89.18	44.60	52.01
HIGH/W	104.00	89.18	57.03	52.01
CO/W	90.33	89.18	51.04	52.01

SELECTION 4

GENERATION 1

	BODY SIZE-OPTIMAL			
	♀ WT	♀W	♂ WT	♂ W
WTH/W	91.11	89.73	51.17	50.75
WTL/W	87.30	82.73	46.28	50.75
WT/WH	89.90	87.23	48.00	45.89
WT/WL	89.90	84.07	48.00	45.62
WT/W	89.90	89.73	48.00	50.75
WTM/W	89.64	89.73	50.03	50.75
WT/WM	89.90	86.80	48.00	49.16

GENERATION 2

BODY SIZE-OPTIMAL			
♀ WT	♀ W	♂ WT	♂ W
96.65	83.26	56.05	41.85
82.24	83.26	42.82	41.85
88.85	90.68	46.05	51.81
88.85	75.28	46.05	33.92
88.85	83.26	46.05	41.85

GENERATION 3

BODY SIZE-OPTIMAL			
♀ WT	♀ W	♂ WT	♂ W
98.74	90.98	61.29	49.92
82.58	90.98	47.18	49.92
91.00	94.52	50.82	56.66
91.00	82.90	50.82	41.79
91.00	90.98	50.82	49.92

GENERATION 4

BODY SIZE-OPTIMAL			
♀WT	♀W	♂WT	♂W
98.05	85.18	61.56	45.03
81.19	85.18	43.63	45.03
86.24	93.55	48.35	55.07
86.24	75.33	48.35	37.71
86.24	85.18	48.35	45.03

GENERATION 5

BODY SIZE-OPTIMAL	
♀ WT	♀ W
103.24	91.12
80.30	51.12
90.39	99.92
90.39	79.52
90.39	91.12

TABLE 9 B

C.I. of Day 1 + 2 in selection experiments for large and small body size (Deviations from unselected).

Experiment No.	Gen.	Large	P	Small	P
2	2	-3.20	0.08	-3.20	0.10
	5	-1.70	0.30	-0.50	0.42
3	4	-0.25	0.50	+0.80	0.07
4(WT)	1	+0.60	0.5	+0.60	0.30
	2	-6.00	0.005	-4.25	0.01
	3	-3.07	0.07	-3.20	0.17
	4	+1.15	0.35	-0.40	0.50
	5	-0.60	0.5	+0.40	0.50
	4(Triple)	-0.70	0.5	-1.00	0.30
4(W)*	1	+2.40	0.03	-0.60	0.5
	2	+5.00	0.02	+1.80	0.14
	3	+0.00	0.00	+2.60	0.15
	4	-1.90	0.03	-1.15	0.15
	5	-1.80	0.40	-0.40	0.50
	4(Triple)	-1.00	0.12	-1.45	0.22

* The sign of the values for the differences in C.I. in this experiment was reversed to make these differences directly comparable with those in other experiments.

Large = large line

Small = small line

P = probability of occurrence of the deviation in C.I.

TABLE No. 9C

SELECTION 4 - DEVIATIONS IN BODY SIZE AND IN COMPETITIVE ABILITY FROM CONTROL (C.I. CONTROL = CONSTANT = 1.96)

DAY 1+2

GEN.	1		2		3		4		5		REGRESSION
	SIZE	C.I.	SIZE	C.I.	SIZE	C.I.	SIZE	C.I.	SIZE	C.I.	OF C.I. on SIZE
WTH-WT	+1.30	+0.04	+8.90	-3.96	+9.10	-1.63	+12.51	-0.21	+12.85	-2.16	-0.14 ± 0.12
WTL-WT	-3.05	+0.04	-4.92	-2.21	-6.03	-1.76	-4.88	-1.76	-10.09	-0.76	+0.11 ± 0.13
WH-W	-3.68	+2.96	+8.71	+2.96	+5.14	+1.44	+9.20	+0.56	+8.80	+0.64	+0.12 ± 0.16
WL-W	-5.40	-0.04	-7.96	-0.24	-8.10	+1.16	-8.58	+0.21	-11.60	+0.76	+0.965± 0.06

The C.I. of the control represents the average superiority of the Pac WT population over the Pac W population; this value has a positive sign in the comparisons involving WT selected lines and a negative one in the comparisons involving lines selected from the Pac white population.

TABLE 9 D

Differences in biomass between lines selected and unselected for body size and a standard unselected competitor in Day 1+2.

	Selection 2			Selection 3	
	Gen 2	Gen 5		Gen 4	
Low/w	-1.91	+2.81	Low/w	+2.80	
High/w	-1.75	+3.90	High/w	+2.00	
Co/w	+3.27	+3.90	Co/w	+2.30	

	Selection 4				
	Gen 1	Gen 2	Gen 3	Gen 4	Gen 5
WTH/W	+3.11	-2.83	+1.28	+2.90	-0.59
WTL/W	+3.00	-0.78	+0.67	+0.57	+2.30
WTM/W	-1.62				
WH/WT	+2.33	+2.34	-3.46	-3.03	-3.17
WL/WT	-3.02	-3.13	-2.15	-2.90	-2.71
WM/WT	+2.14				
WT/W	+2.69	+3.69	+3.50	+1.85	+2.08

Biomass was calculated by adding the difference of the logs of body size and the log of the difference in the number of flies of each genotype hatched in days 1 and 2.

TABLE 9 E

VIABILITY AND TOTAL PRODUCTIVITY OF LINES SELECTED AND UNSELECTED FOR BODY SIZE, MEASURED UNDER COMPETITIVE CONDITIONS.

SELECTION 2

	GENERATION 2					GENERATION 5				
	%		TOTAL	2		%		TOTAL	o	
	WT	W	WT+W	TOTALS	HET.	WT	W	WT+W	TOTALS	HET
LOW/W	53.47		27.40	0.59	1.11	57	43	21.60	2.37	2.34
HIGH/W	50	50	28.20	0.00	2.59	62	38	23.60	6.64	2.03
PAC/W	46	54	27.40	0.88	2.49	63	37	24.00	8.53	4.72
F RATIO			0.00					1.00		

SELECTION 4

	GENERATION 1					GENERATION 2					GENERATION 3					GENERATION 4					GENERATION 5				
	%		TOTALS	χ^2		%		TOTAL	χ^2		%		TOTAL	χ^2		%		TOTAL	χ^2		%		TOTAL	χ^2	
	WT	W	WT+W	TOTALS	HET.	WT	W	WT+W	TOTALS	HET	WT	W	WT+W	TOTALS	HET.	WT	W	WT+W	TOTALS	HET	WT	W	WT+W	TOTALS	HET
WTH/W	51	49	23.8	0.07	3.95	47	53	21.0	0.46	2.91	52	48	27.4	0.18	2.75	52	48	23.4	0.21	3.85	47	53	19.2	0.33	0.95
WTL/W	45	55	23.6	1.03	10.80*	41	59	22.6	3.90*	0.489	43	57	21.8	2.06	1.77	53	47	21.6	0.33	0.62	47	53	20.0	0.36	2.07
WT/WH	43	57	22.0	2.32	1.09	42	58	21.2	3.05	3.47	52	48	27.8	0.18	0.87	52	48	20.2	0.25	4.31	44	56	24.4	1.60	2.83
WT/WL	50	50	22.2	0.01	1.31	55	45	22.8	1.26	0.59	50	50	23.8	0.00	2.33	55	45	25.6	1.53	1.31	46	54	20.4	0.63	4.78
WT/W	50	50	24.3	0.00	12.62	53	47	18.6	0.27	1.05	50	50	21.6	0.00	3.34	46	54	25.0	0.97	0.45	51	49	19.6	0.04	1.72
	45	55	27.0	1.25	4.36																				
	45	55	25.4	1.33	1.17																				
F RATIO			1.16					0.62					3.00*					2.309					1.60		

generation of selection. This could be the result of the large variation in the competitive ability of the control, between generations. But this same variation can be invoked to disprove any observed reduction in the competitive ability of the selected lines in the first 2 generations of selection.

When we studied our model of competition we considered that the biomass produced per unit of time was the best indicator of fitness available. (table 9D) Our competition index does not take account of the differences in body size between the competitors. However, it is not difficult to see that any reduction in the competitive ability of the small line will be reinforced by an inferiority in body size. In the large line however an apparent inferiority in competitive ability could be compensated by the increase in body size.

Bearing in mind this relationship between the competitive index and biomass it is clear that the device of the competitive ability of Day 1 + 2 as an indicator of fitness is perfectly justified.

Ideally we would like to describe the functional relationship of body size with fitness in terms of a curve or regression line. Regression lines were fitted and the regression coefficients are indicated in Table 9C. Due to the above mentioned variation in the competitive ability of the control a correction was introduced which consisted in using as control the average superiority of the WT over the white. This value is equal to +1.96.

None of the regression coefficients estimated deviated significantly from zero.

(ii) The results of the study of the competitive ability of the line selected for large and small body size, expressed as deviations from unselected, show a considerable degree of variation and no clear trend is visualized concerning a possible "fall-off" in fitness (see Table 9B). To large deviations in body size corresponded little or no reduction in competitive ability. Certainly, significant decreases in competitive ability were observed but they were not consistent with the progress of selection.

(iii) The selected lines showed considerable changes in body size which can be traced back to changes in some physiological parameters. The results of simulation of the effects of these changes on fitness showed that biomass and development time could be substantially affected leading to change in fitness. If these changes are not observed in practice the distribution of the biomass between the individuals composing a selected line must be changed in such a way that the C.I. of Day 1 + 2 is relatively little affected. In other words not only the mean value of such physiological parameters would be affected but also its variance. If this is true then the changes in fitness consequent to changes in physiological parameters would only be noticeable when the deviation of the mean is large enough to overcome the effects of the different distribution of biomass between the individuals of a selected line. However, when this variance is equal in

both competitors as in the case of competition between Pac WT and W. The importance of this factor is likely to be very much restricted.

We can see the need for models of competition involving the variance in body size of the competing individuals. Only when these models are developed will we be able to predict with exactitude the results of changes in competitive ability with selection.

C - PRODUCTIVITY

The differences in productivity are shown in the respective tables as well as the significance of their deviations from the control.

(i) Total productivities were not affected with one possible exception, that of generation 3 of sel. 4.

(ii) Early productivity was generally higher for the low lines than for the high lines with the control occupying an intermediate position. This effect is probably a consequence of the differences in the rate of "cropping" of the yeast population (Low < Co < H), associated with differences in critical size. A detailed discussion of this topic is presented under the heading of "competition between large and small lines".

D - VIABILITY

With one exception, that of the WT low line in Gen. 2 of sel. 4, this parameter was not affected when compared with the same value for the standard competitor. This fact points in the direction that the reduction of the fitness of selected lines is not caused by a reduction in viability. (see tables 9E and 16).

TA BLE No.10.

SELECTION 4 - GENERATION 1

	DAY 1 and 2								DAY 3							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTL/W	38.88	46.00	-7.11	4.75	-4.00	+8.75	+2.0	4.0	42.80	44.15	-1.35	-0.58	8.50	-9.08	+1.6	8.8.
WTH/W	48.00	47.50	+0.50	14.00	-9.00	+23.00	+2.0	2.4	40.61	41.50	-0.88	3.44	5.38	-1.94	+1.4	13.0*
WTM/W	32.80	46.67	-13.86	-8.75	10.50	-19.25*	-0.6	4.2	40.84	41.62	-0.78	14.37	3.28	+11.08*	+2.6	11.4
WT/WL	53.88	53.25	+0.63	15.25	11.00	+4.25	+2.0	8.0	60.50	47.60	+12.90	16.69	11.50	+5.19	-1.0	10.2
WT/WH	53.25	47.63	+5.61	19.25	19.66	-0.41	-1.0*	5.8	48.09	57.31	-9.22*	16.16	20.88	-4.71	-2.0	11.2
WT/WM	55.70	56.50	-8.80	16.28	19.33	-3.04	-0.8	7.2	53.76	54.81	-1.04	20.00	10.78	+9.21*	-2.6	11.8
WT/W	57.63	50.16	+7.46	18.33	15.80	2.53	+1.4	4.8	48.82	48.26	+0.56	15.22	9.95	+5.27	+0.50	9.7
F RATIO							2.42*	1.38							1.84	0.79

DIFF = difference in average body size between the WT and the W competitors.

C,I. = competitive index of WT in relation to W. PRD = number of individuals hatched per culture irrespective of their genotypes.

THESE SYMBOLS ARE USED IN ALL COMPETITION EXPERIMENTS WITH THE SAME MEANING.

SELECTION 4 - GENERATION 1 - cont'd

	DAY 4								DAY 5+							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTL/W	42.00	50.16	-8.16	1.80	12.76	-10.96	-2.2	7.8	61.00	50.33	+10.66	18.00	26.25	-8.25	-1.40	3.0
WTH/W	43.00	44.40	-1.40	8.33	11.25	-2.90	-1.2	6.4	61.00	61.71	-0.71	2.00	18.00	-16.00	-1.0	2.2
WTM/W	35.16	40.45	-5.28	4.83	8.45	-3.62	-3.8	8.6	47.66	51.57	-3.90	42.66	19.33	23.33	-1.4	3.8
WT/WL	59.66	53.25	+6.41	28.00	15.80	+12.20	-1.0	2.8*		75.00		28.00	12.33	15.66	-0.5	1.2*
WT/WH	46.25	57.85	-11.60	23.00	19.66	+3.33	-0.4	3.6	51.50				7.66	+0	+0.5	1.4
WT/WM	56.00	51.00	+5.00	10.66	7.00	+3.66	+0.50	3.6	80.00	70.50	9.50	13.75	16.33	-2.58	+0.4	2.4
WT/W	55.43	53.38	+2.05	6.38	5.34	1.03	-1.20	7.0	50.14	42.57	7.57	23.00	18.20	4.80	-0.56	2.9
F RATIO							1.30	1.98							0.77	1.06

TABLE No.11

SELECTION 4 - GENERATION 2

	DAY 1 + 2								DAY 3							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTH/W	45.50	37.28	+8.22	18.00	-5.80	+23.80**	-2.00**	3.20	45.11	26.93	+18.18*	-3.40	-2.16	-1.24	-2.20	8.60
WTL/W	40.33	37.00	+3.33	28.00	18.00	+10.00	-0.25**	3.40	27.13	28.00	-8.07	-13.4	-9.28	-5.12	-0.60	8.60
WT/WH	45.00	47.58	-2.58	15.25	20.00	-4.75	-1.00*	7.80	36.62	47.88	-11.26	8.57	6.25	+2.32	-1.20	7.20
WT/WL	43.23	39.62	+3.61	15.22	10.28	+4.94	+2.20	8.20	41.61	19.80	+21.81**	10.80	0.25	+10.55	+2.00	7.20
WT/W	36.27	37.57	-1.30	3.33			+4.00	6.8	28.33	34.55	-6.22	7.20	-0.11	+7.31	-0.80	6.40
F RATIO							3.6*	1.12							1.0	0.35

SELECTION 4 - GENERATION 2 - cont'd

	DAY 4								DAY 5+							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTH/W	38.37	27.50	+10.87	-0.27	2.00	-2.27	+1.4*	6.20	68.00	47.50	20.50	-11.00	7.66	-18.66	+1.00*	3.00
WTL/W	29.66	24.54	+5.12	0.33	6.46	-6.13	-3.75	6.60	53.00	61.5	-8.50	18.00	28.00	-10.00*	+0.80*	2.80
WT/WH	30.25	41.22	-10.97	-10.66	-0.25	-10.41	-2.33	4.20	50.80	64.00	-13.20		41.66		-0.25	2.20
WT/WL	31.75	31.62	+0.13	-11.00	7.12	-18.12	-2.66	4.80	56.50	52.00	+4.50	35.50	25.50	+10.00	-0.25	2.60
WT/W	17.33	35.00	-17.67	-1.33	-13.37	+12.04*	-2.33	3.8		40.00		7.00	16.25	-9.25	-1.00	1.60
F RATIO							3.07	0.25							1.5	0.62

TABLE No.12.

SELECTION 4 - GENERATION 3

	DAY 1 + 2								DAY 3							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTH/W	54.00	43.00	+11.00	10.50	2.00	+8.50	+0.33	1.80*	47.13	38.91	+8.22	11.94	9.68	+2.26	+1.80	14.20
WTL/W	46.75	46.50	+0.25	17.75	22.33	-4.58	+0.20	6.20	40.22	48.42	-8.20	4.29	10.81	-6.52	-1.80	12.20
WT/WH	51.91	52.33	-0.42	11.55	23.00	-11.45*	+3.40	5.00	45.30	51.15	-5.85	11.20	18.00	-6.80	-2.20	12.20
WT/WL	51.43	46.58	+4.85	20.89	11.64	+9.25*	+0.80	13.2*	53.45	38.44	+15.01*	16.58	7.15	+9.43	+0.20	9.00
WT/W	45.00	53.00	-8.00	16.00	13.00	+3.00	+3.40	5.8	47.11	50.42	-3.31	9.22	11.40	-2.18	-0.40	11.60
F RATIO							1.68	0.11							0.94	1.00

SELECTION 4 - GENERATION 3 - cont'd

	DAY 4								DAY 5+							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTH/W	42.37	42.80	-0.43	18.41	8.92	+9.49*	-0.60	8.60	43.00	48.00	-5.00	9.60	8.28	+1.32	-0.50	2.80
WTL/W	50.00	46.42	+3.58	-3.50	10.6	-14.10	-1.60	3.20	33.00						+1.00*	0.20
WT/WH	52.80	52.25	+0.55	19.14	13.47	+5.67	-4.00	10.00	52.00	56.50	-4.50				-0.33	0.60
WT/WL				40.00	7.33	+32.67*	-1.75	1.40*	52.00						+1.00*	0.20
WT/W	70.00	58.00	+12.00	8.00	12.36	-4.36	-2.40	3.60	28.00	28.00	0.00		28.00		-0.50	0.6
F RATIO							0.05	3.67*							0.38	3.23*

TABLE No.13.

SELECTION 4 - GENERATION 4

	DAY 1 + 2								DAY 3							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTH/W	53.66	49.50	+4.16	14.80	5.66	+9.14	+1.75	4.20	40.25	42.00	-1.75	15.70	4.12	+11.58*	-1.00*	6.60
WTL/W	24.12	38.00	13.88*	2.00	-7.80	+9.80	+0.20	3.80	20.63	36.57	-15.94**	-4.00	-2.83	-1.17	+1.80	7.00
WT/WH	41.70	68.66	-29.26***	16.60	25.50	-8.90	+2.50*	4.00	39.85	43.80	-3.95	4.75	20.00	-15.25*	+1.40	6.20
WT/WL	42.16	33.00	+ 9.16	7.50			+1.75	1.80	45.46	29.30	+16.16*	4.71	4.00	+ 0.71	+2.6	8.60
WT/W	48.55	42.25	+ 6.30		3.25		+0.60	3.80	42.44	41.00	+1.44	-1.07	3.28	- 4.35	+0.80	8.00
F RATIO							1.00	0.45							1.86	0.33

SELECTION 4 - GENERATION 4 - cont'd

	DAY 4								DAY 5+							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTH/W	59.11	45.00	+14.11	3.20	11.00	-7.80	1.00	6.60	57.20	45.83	+11.37	6.11	3.10	+3.01	-0.80*	6.40
WTL/W	34.72	29.64	+5.08	-11.66	1.37	-13.03	-1.60*	7.20	43.85	39.16	+4.69	6.50	18.00	-11.50**	+0.80*	3.60
WT/WH	35.00	49.80	-14.80	6.42	19.00	-12.58	+0.60	4.20	27.25	52.86	-25.61	3.20	16.37	-13.17	-2.80	6.40
WT/WL	35.30	34.75	+0.55	2.30	-5.77	+8.07	+0.60	7.40	65.50	41.92	+23.58**	6.60	6.20	0.40	-1.60	8.00
WT/W	35.66	34.66	+1.00	1.16	-3.28	4.44	+0.40	5.60	36.50	47.07	-10.57	8.42			-4.00	7.60
F RATIO							1.28	0.65							4.04*	0.40

TABLE No.14.

SELECTION 4 - GENERATION 5

	DAY 1 + 2								DAY 3							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTH/W	59.33	46.18	+13.15*	23.00	15.85	+7.15	-0.20	7.00	44.60	43.28	+1.32	19.27	8.60	+10.67*	-1.40	7.80
WTL/W	39.00	55.87	-16.87*	10.57	10.11	-20.68*	+1.20	8.00	32.30	43.38	-11.08*	6.25	14.20	-7.95	-1.80	7.40
WT/WH	50.00	45.20	+4.80	10.57	33.00	-22.43***	+2.60	5.00	54.33	57.25	-2.92	18.00	28.71	-10.71*	0.00	6.00
WT/WL	56.92	29.25	+27.67**	13.55	-5.16	+18.71**	+1.20	7.60	61.00	31.45	+29.55***	12.58	8.12	+4.46	-1.20	6.40
WT/W	55.70	52.07	+3.63	14.16	18.80	-4.64	+0.80	8.00	51.00	52.22	-1.22	14.44	5.70	+8.74	-1.20	6.80
F RATIO							1.20	0.55							0.23	0.20

SELECTION 4 - GENERATION 5 - cont'd

	DAY 4								DAY 5+							
	♀ Size			♂ Size			C.I.	PRD	♀ Size			♂ Size			C.I.	PRD
	WT	W	DIFF	WT	W	DIFF			WT	W	DIFF	WT	W	DIFF		
WTH/W	55.42	44.25	+11.17	20.80	18.00	+2.80	+0.60	4.20	46.33	50.20	-3.87	23.00	2.00	+19.00	-0.25	2.20
WTL/W	35.25	36.00	-0.75	2.00	7.00	-5.00	-0.50	2.60	35.50	64.75	-29.25**	15.50	37.50	-22.00	-0.40	2.00
WT/WH	40.80	56.25	-15.45*	14.36	26.06	-11.70*	-2.40	8.8	52.00	69.46	-17.46		36.33		-2.80	4.80
WT/WL	68.75	25.50	+43.25**	25.00	0.00	+29.00***	-1.00	4.4	79.00	46.00	+33.00*	42.50	28.00	+14.50	-1.33*	2.00
WT/W	55.00	49.50	+5.50	4.00	12.00	-8.00	+0.40	2.8	56.50	47.50	+9.00	15.00	35.00	-20.00	+0.50*	2.00
F RATIO							0.75	2.00							2.92*	1.63

TABLE No.15.

SELECTION 3

	DAY 1 + 2				DAY 3				DAY 4				DAY 5			
	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD
HIGH/W	+1.00		+0.75	1.00	+4.50		-1.00	0.80	+17.53*	+5.50	-0.80	10.80	+5.60	+16.41***	-0.40	12.40
LOW/W			+1.80	1.80*	+8.75	-2.16	+1.50	3.60	-17.37**	-6.58	+1.20	8.80*	-5.19	-8.75	-5.40*	11.40
CO/W			+1.00	0.20	+7.5	+17.00	0.00	1.20	+0.22	-5.85	0.00	13.20	-1.73	+9.85**	-1.00	12.20
F RATIO			0.90	6.80*			1.48	3.06			1.50	1.42			3.27*	0.06

TABLE no. 16

	BODY SIZE OPTIMAL		%		TOTAL	χ^2	
	WT	W	WT	W	WT+W	TOTALS	HET
HIGH/W	21.85	88.70	48	52	25.00	0.20	0.62
LOW/W	83.51	88.70	48	52	25.60	0.28	1.86
CO/W	89.21	88.70	48	52	26.80	0.12	0.32
F RATIO					0.46		

TABLE No.17

SELECTION 2 - GENERATION 2

	DAY 1 + 2				DAY 3				DAY 4				DAY 5			
	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD
LOW/W	-14.70*	-9.87	-0.60	7.40	+2.18	-5.94	+1.00	9.80	-19.31**	-2.45	+1.20	9.60			+0.50*	0.60
HIGH/W	+8.75*	-5.25	-0.60	7.80	+1.29	-2.90	+1.20*	10.00	-4.03	-20.58	-0.40	7.20	-12.33**	-10.00*	-0.67	2.80
CO/W	2.14	-0.09	+2.60	11.80	-1.59	-0.83	-2.00	10.00	26.00	+5.80	-1.20	4.00			-1.60	1.60
F RATIO			1.36	0.88			3.40	0.00			1.70	2.19			1.82	1.20

TABLE No.18.

SELECTION 2 - GENERATION 5

	DAY 1 + 2				DAY 3				DAY 4				DAY 5+			
	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD
LOW/W	-6.14	-9.90	+1.80	4.80	-5.07	-0.97	+1.60	8.40	-17.23	+5.37	+0.20	5.40	-0.21	-3.25	-0.40	4.00
HIGH/W			+4.00	1.60	+29.22*	+3.42	+2.80	6.80	+5.30	+5.00	+3.20	8.00	-12.64*	-3.74	-2.00	7.20
PAC/W	+16.08		+4.50	1.60	+14.58*	-3.00	+2.20	6.00	+8.60	-3.10	+2.80	10.00	-1.80	+9.76*	-2.00	6.00
F RATIO			1.73	1.68			0.23	0.45			1.44	1.67			1.10	0.76

TAILS OF THE DISTRIBUTION VERSUS THE MEDIAN

(table 10)

The results of this experiment/show that:

(i) Body size of WTM and WM exhibit significant deviations from the unselected white population in days 1 + 2 and 3. Since the sign of these deviations is not constant this must be an artefact.

(ii) The competitive ability of WTM is inferior to that of the unselected and both the tails, although not significantly so. The WM line has a value of C.I. intermediate to that of both tails.

(iii) The values for productivity in Day 1 + 2 and for total productivity are not different for the tails and the medians.

(iv) The conclusion from this experiment is that no differences in competitive ability could be detected between individuals exhibiting maximum and minimum deviation from the mean of body size in the unselected population.

RELAXATION OF SELECTION FOR BODY SIZE

In the sel 1 experiment selection was relaxed at generations 4 and 9 under a variety of circumstances, with changes from competitive conditions (10 eggs/vial) to optimal conditions and vice-versa.

Two experiments were carried out in generation 4:

Expt.1 - Mating was randomised in this experiment by choosing partners at random. Also, egg production was eliminated as a component of fitness by standardizing the contribution of eggs from each female, to the next generation.

Expt. 2 - This experiment differed from the previous one in that both mating choice and egg production were not controlled.

The results of these experiments are shown in Tables 21 and 22.

Three experiments were carried out in generation 9:

Expt. 1 - Relaxation under different levels of crowding.

Expt. 2 - Relaxation in bottles

Expt. 3 - Relaxation in population cages.

The results of these experiments are shown in Tables 23 and 24.

The results of relaxation of selection in the sel. 2 experiment are shown together with the results of the inbreeding experiment.

A. BODY SIZE

(i) Relaxation from Gen.4 under a wide range of conditions had no effect in reducing the deviation of the selected lines from the unselected.

(ii) There was a mild reversion to the mean value when selection was relaxed under cage or bottle conditions in generation 9. This reversion amounted to 10% of the difference in body size between the High and the Low lines.

A closer look at Table NO.24 reveals that this reduction in the deviation between the large and the small lines is entirely a consequence of a reversion in the small line, this reversion being more marked under cage conditions than under bottle conditions. The large differences between the average body of the controls in the bottle and the cage experiment can probably be accounted for by the different origin of these populations: the bottle control is derived from the control population started at the beginning of the selection experiment and maintained under optimal conditions, and the cage control is represented by our base population, Pacific WT.

(iii) The results of relaxation under varying crowding conditions provided us with an estimate of the average reduction of body size in the three lines (large and small, and unselected), as can be observed from Table 22. At the higher crowding levels (30,50 and 70 eggs/vial) the selected lines are proportionately more reduced than the unselected.

(iv) Relaxation of selection in the sel. 2 expt. had little or no effect in bringing the mean value of body size of the selected lines towards the unselected level.

B.- VIABILITY

(i) Viability was affected by crowding, the unselected lines showing the highest viability at 50 and 70 eggs/vial respectively. These results have to be considered in connection with the fact that the average crowding intensity in the population cage was estimated to correspond

30 eggs/vial.

(ii) Relaxation improved the viability (measured under OPTimal) of the lines relaxed under bottle and cage conditions and brought it back to the level exhibited by the unselected population.

(iii) The viability of the low line of sel.2 (measured under competitive conditions) deteriorated when compared with the corresponding estimate for generation 5 of selection.

TABLE No.21

SELECTION 1 - RELAX 4 (EXPT. 1).

Gen 1		Gen 2		Gen 3		Gen 4		Gen 5	
Line	Size	Line	Size	Line	Size	Line	Size	Line	Size
H_4OPT	97.30	H OPT	93.50	H OPT^2	95.40	H OPT^3	93.35	H OPT^2-CT-OPT	95.80
				H OPT-CT	87.80	H OPT^2-CT	70.00	H OPT^2-CT^2	71.55
		H CT	65.44	H CT^2	81.45	H CT^3	70.35	H CT^2-OPT-CT	72.80
				H CT-OPT	92.20	H CT^2-OPT	93.75	H CT^2-OPT^2	90.10
L_4OPT	81.70	L OPT	80.87	L OPT^2	77.34	L OPT^3	79.60	L OPT^2-CT-OPT	83.60
				L OPT-CT	70.50	L OPT^2-CT	69.00	L OPT^2-CT^2	63.60
		L CT	63.55	L CT^2	74.42	L CT^3	57.95	L CT^2-OPT-CT	62.25
				L CT-OPT	82.90	L CT^2-OPT	80.95	L CT^2-OPT^2	72.35
CO_4OPT	75.33	CO OPT	86.55	CO OPT^2	88.20	CO OPT^3	87.60	CO OPT^2-CT-OPT	86.52
				CO OPT-CT	81.60	CO OPT^2CT	65.65	CO OPT^2-CT^2	73.00
		CO CT	68.11	CO CT^2	77.50	CO CT^3	66.00	CO CT^2-OPT^2	87.35
				CO CT-OPT	90.60	CO CT^2-OPT	92.20	CO CT^2-OPT^2	87.35

H_4, L_4 and CO_4 refer to the selected and unselected lines at generation 4 of selection. The symbols OPT and CT stand for Optimal and Competitive conditions of growth; the level of crowding in the competitive cultures was 10 eggs/vial. The symbols OPT and CT also indicate the history of a given line; for example L OPT^2-CT refers to a low line which was relaxed under optimal in the first two generations of relaxation and under competitive conditions in the third generation.

TABLE No.22

SELECTION 1 - RELAX (EXPT.2).

GEN.1		GEN.2		GEN.3	
Line	Size	Line	Size	Line	Size
L_4OPT	81.70	L OPT	77.00	L OPT^2	63.75
				L OPT^2-CT	17.35
		L CT	18.10	L CT^2	30.00
				L CT-OPT	75.50
H_4OPT	97.30	H OPT	96.00	H OPT^2	76.05
				H OPT-CT	32.55
		H CT	35.35	H CT^2	43.80
				H CT-OPT	81.35
CO_4OPT	75.33	CO OPT	86.55	CO OPT^2	69.85
		CO CT	26.95	CO CT^2	26.95

The symbols adopted in this experiment are the same as in table221.

Table No.23.

RELAX - 9 (EXPT.1) - CROWDING (CT-OPT)

% REDUCTION IN BODY SIZE.

No.Eggs	H		CO		L	
	Size	Viability	Size	Viability	Size	Viability
70	66.90	0.54	52.85	0.64	59.70	0.55
50	61.25	0.69	47.70	0.71	63.85	0.60
30	52.60	0.76	35.15	0.67	43.40	0.43
20	36.80	0.75	31.90	0.74	26.80	0.65
9*	1.65	0.88	7.35	0.93	3.25	0.93
6*	-6.60	0.98	-6.50	0.96	-4.30	0.81
3*	-2.67	0.9	16.22	0.93	7.22	0.80

*Newly hatched larvae used instead of eggs.

TABLE No.24

SELECTION 1 - RELAX 9

			EXPT 2 BOTTLES (5 GEN)	EXPT 3 CAGES (3 MONTHS)
	L_9	60.00	64.54	68.64
Lines	H_9	100.95	93.78	97.08
	CO_9	83.70	79.34	72.58
H-L		40.95	29.34	28.44
H-CO		17.25	+14.44	+21.80
L-CO		-23.70	-14.80	-6.64

COMPETITION UNDER VARIABLE PROPORTION BETWEEN HIGH AND LOW LINES (Sel.4).

This experiment was designed to test the hypothesis that High and Low lines differed in

(i) Feeding rate H > L

(ii) Critical size H > L

These differences could generate similar development times for both lines when in competition with each other. Since this development time would be achieved through physiologically different ways, this should be reflected by differences in body size. Moreover, since differences in feeding rate would generate different ecological situations, this could be reflected in the productivity and in the competitive ability. The easiest way to reveal these differences is to vary the frequency of the competing individuals and study the consequences of this variation on the C.I. and productivity.

This experiment consists of two independent but contemporary experiments: competition between WTH and WL (Expt.1) and competition between WTL and WH (Expt.2). The results of both are summarized in Table 25.

A. BODY SIZE

The differences in body size between the competitors are always marked within days.

B. COMPETITIVE ABILITY

(i) The C.I. is variable within experiments with variable proportion of the competing genotypes. The significance of the deviations of the C.I. from zero is shown in the Table. We can see that in experiment 1

only the 10/30 level is significantly different from zero (Days 1 + 2 and 3); in experiment 2 the 30/10 level is significant in day 3 and the 20/20 in day 4. These differences indicate clearly that the frequency of the competing genotypes affects their fitness; in other words there is frequency-dependent selection, although the results cannot be explained by the easy and convenient formula of "the rarest, the fittest".

(ii) If we look at the C.I. figures for Day 3 (since the productivity of Day 1 + 2 is relatively small and more affected by sampling variance), we can see that in experiment 1 the C.I. and the frequency of WTH are positively correlated. In other words, as the proportion of the low line increases the competitive ability of the wild-type individuals compared with the whole ones, decreases. In both experiments the WT lines are inferior to their white competitors.

(iii) The magnitude of the oscillations around zero, exhibited by C.I. in different days (within experiments and within proportions) is positively correlated with the frequency of the low line. This suggests that the expression of the inferiority of the WT lines in relation to the white ones is dependent on the amount of food available in the cultures. The larger this amount is the better expressed the differences in C.I. will be. If the low lines are slow-feeders then the higher their frequency is the greater the oscillations in C.I. This is what we find in these experiments. Another point supporting this conclusion is connected with the differences in early productivity between corresponding levels in Experiment 1 and Experiment 2. The cultures in Experiment 2 have a

higher early productivity than the parallel cultures in Expt. 1, although the total productivities do not differ much. The higher early productivity suggests that there is more food available in the cultures of experiment 2 than in experiment 1, therefore the differences in C.I. should be more marked. Indeed they are, not only in the amplitude of the oscillations but in the number of levels which exhibit significant differences (10/30 level in expt. 1; 30/10 and 20/20 in expt. 2).

A qualification that must be made at this stage concerns the results of simulation of these conclusions in a computer. If we assume that the changes in feeding rate and in critical size, of the 4 strains under study, are fixed, i.e. independent of the intensity of competition (therefore independent of the frequency of the competing genotypes) the results of simulation, do not fit the observed data. Therefore we must consider the possibility of the differences in feeding rate and in critical size being dependent on the intensity of competition. In other words we shall have to consider what we mean exactly by the terms feeding rate and critical size and how much is the expression of these "characters" a function of the environment.

C - PRODUCTIVITY

(i) Total productivity - The two experiments show some contrast in this respect. Although the final proportions never deviate from the initial ones (χ^2 N.S.) the total productivity of all but the 10/30 level in Expt.1 is significantly smaller than the productivity of the 20/20 level. Expt.2 does not show these differences in productivity.

(ii) Day-to-day productivity. The productivities of Day 1 + 2 and Day 3 in Expt.1 and that of Day 1 + 2 in Expt.2 are positively correlated with the frequency of the low line, as we would expect if the low lines were slow-feeders.

(iii) The fact that in both experiments the early productivity of the culture is positively correlated with the frequency of the low line indicates that the increased development time of the High line under pure and culture conditions is not only caused by an intrinsic increase in development time (say, an increase in critical size) but also by the higher rate of cropping of the yeast population exhibited by the High line. The early productivity of the several levels in expt. 1 is smaller than the corresponding levels in Expt.2. Since the total productivities are similar for both experiments, these differences must be genuine. If we assume that the two unselected populations (WT and W) differed in some factor that generated a difference in their competitive ability, e.g. in feeding rate. We can imagine that selection for small body size in the WT population and selection for large body size in the white population has in relation to their feeding rate made these two populations more similar.

Conversely, selection for small body size in the W population and large size in the WT population has enlarged the gap between these two strains as far as feeding rate is concerned. In this way competition between WTH and WL will involve individuals that are more different than when competition is between WTL and WH. This could be reflected in differences

in productivity between the 2 experiments. It would also explain the differences in total productivity between the several levels of Expt.1.

SELECTION FOR SHORT DEVELOPMENT IN LINES SELECTED FOR LARGE AND SMALL BODY SIZE.

By performing these selection experiments we intended to simulate the result of different types of selection pressure likely to be exerted on individuals of lines selected for body size and observe the effects of these pressures on body size and on competitive ability.

Since development time is the most important component of fitness in organisms like Drosophila (LEWONTIN, 1965) we shall consider the selection for fast development under competitive conditions in the selected lines (sel.2 and sel.4, WT) as well as the unselected (control). The results of these comparisons after 3 generations of selection are summarized in Table 26.

(i) Back selection for development time on lines of the sel. 2 experiment eliminated any previous differences in competitive ability between these lines and the unselected. The same was not observed in the sel.4 experiment where the High line still showed some inferiority (Day 4).

(ii) The analysis of differences in productivity (both early and total) revealed an inferiority on the part of the high line in the sel. 4 experiment. This inferiority must reveal an increased development time since the total productivity is significantly reduced.

(iii) Viability was reduced only in the High line of sel. 2.

(iv) Back selection for development time was not effective in bringing the average body size back to its unselected value.

(v) The judgement on the differences in C.I. between selected and unselected must be cautious since the performance of the control population is very poor (negative values for C.I. in Day 1 + 2 and Day 3), therefore more experiments are required before any final conclusion is made about the effects of back selection for fast development time on fitness.

BACK SELECTION FOR BODY SIZE

This selection was carried out under optimal conditions and using the same selection intensity adopted for forward-selection for large and small body size.

(i) Back selection for body size was effective in reducing rapidly the deviation from unselected in both selected lines. Unfortunately our expectations about the response to the last round of back selection were not fulfilled reason why the unselected level was not reached by the selected lines.

(ii) The unselected population does not differ in C.I. from the selected lines, up to Day 5, when both selected lines become superior to the unselected. However if we pool the C.I.'s from Day 1 to Day 4 we can see that the unselected has the highest C.I., although not significantly so.

(iii) There are no significant differences in viability or in productivity between the 3 strains.

(iv) As for selection for short development time, no data is available on the differences in body size measured under competitive conditions. This gap should be filled in the future to allow us to have more insight into the physiological mechanisms involved in the response to back selection for both characters.

TABLE No.25.

COMPETITION AT VARIABLE PROPORTIONS BETWEEN LARGE AND SMALL LINES.

	DAY 1 + 2				DAY 3				DAY 4				DAY 5				% TOTAL			χ^2	
WTH/WL	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	WT	W	WT+W	TOTAL	HET
40/0				2.2				8.4				8.8				3.0			22.4*		
30/10	+24.66*	-1.67	+0.012	1.6	17.25**	33.07**	+0.088	10.4	23.02**	27.42***	-0.105	8.4	9.00	14.60	-0.006	2.0	74	26	22.4*	0.05	1.99
20/20	+26.34		+0.028	1.4	23.46***	29.80**	+0.020	10.8	26.98***	29.84***	-0.031	12.2	16.34	18.15**	+0.06	3.6	49	51	28.0	0.03	0.70
10/30	+1.50		-0.071*	1.6	28.41***	32.60**	-0.158*	13.4	27.42***	28.36**	+0.021	8.6	9.40	35.40*	+0.121	2.8	29	71	26.4	1.01	1.49
0/40				4.8				12.2				4.6**				1.8			23.4*		
F RATIO				2.4				1.0				2.0				0.7			3.99*		
WTL/WH																					
40/0				7.6				8.2				6.4				1.6			23.8		
30/10	-31.35***	-33.20***	+0.054	4.8	-14.72*	-15.76	-0.253	12.0	-18.80**	-24.72***	+0.167	4.6		-15.00*	+0.068	1.6	74	26	22.8	0.10	3.40
20/20	-12.17	-21.16	+0.005	3.2	-2.33	-13.86*	+0.09	9.6	-15.57**	-13.36**	-0.185*	8.8	-25.08**	-10.40	+0.111	2.8	47	53	24.2	0.40	2.75
10/30	-1.50		-0.018	1.4	-8.92**	16.00	-0.001	12.0		5.24	-0.028	7.8	-13.66	-45.30	+0.076	3.0	17	83	24.2	3.77	0.76
0/40				4.4				12.4				4.8				1.6			23.2		
F RATIO				1.25				1.00				0.79				0.56			0.13		

TABLE No.26.

BACK SELECTION 2 - DEVELOPMENT TIME*

	DAY 1+2		DAY 3		DAY 4		DAY 5+		%		TOTAL	χ^2	BODY SIZE-OPTIMAL		
	C.I	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	WT	W	WT+W	TOTALS	HET	B'SEL	RELAX
H/W	-1.20	4.80	-2.20	12.00	-1.50	3.20	+0.6	2.60	41	59	22.60	3.90	1.49	103.30	103.80
L/W	+0.25	1.40	-1.20	12.00	0.00	6.00	+2.00	0.80	50	50	20.20	0.00	7.45	69.06	68.76
WT/W	-0.40	4.00	-2.00	10.80	-1.60	5.20	+1.00	2.20	43	57	22.20	2.02	1.28	90.86	87.05
F RATIO	0.54	2.32	0.24	1.00	0.76	0.87	0.58	3.60			0.65				

BACK SELECTION 4 - DEVELOPMENT TIME*

	DAY 1 +2		DAY 3		DAY 4		DAY 5		%		TOTAL	χ^2	BODY SIZE-OPTIMAL		
	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	WT	W	WT+W	TOTALS	HET	B'SEL	RELAX
H/W	+1.00	4.00	-1.50	6.00*	-1.00*	6.00	+0.67	1.50	46	54	17.50**	0.51	1.73	94.22	102.70
L/W	-0.50	1.00	-0.40	10.80	-0.60	8.60	-0.80	2.40	46	54	22.80	0.87	2.28	72.60	81.30
WT/W	-0.25	1.40	-0.60	12.00	+2.6	8.60	-0.60	4.60	49	51	26.60	0.07	3.39	84.00	88.70
F RATIO	0.74	1.60	0.20	0.27	3.50	0.69	0.90	3.08			11.90***				

TABLE No.26A

BACK SELECTION 4 - BODY SIZE*

	DAY 1+2		DAY 3		DAY 4		DAY 5+		% TOTAL			χ^2	BODY SIZE-OPTIMAL		
	C.I.	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	WT	W	WT+W	TOTALS	HET	B'SEL	RELAX
H/W	-1.00	3.00	0.00	9.00	-0.75	8.00	+3.80*	3.00	42	58	22.40	2.03	2.56	85.17	102.70
L/W	+0.25	1.80	+1.00	5.80	-1.60	7.00	+0.40*	5.80	42	58	20.40	2.61	0.26	76.23	81.30
WT/W	-1.00	4.20	+0.80	10.00	0.00	4.80	-2.33	3.00	47	53	21.2	0.54	1.39	82.37	88.70
F RATIO	0.29	1.45	0.13	1.86	0.33	0.57	5.36*	0.75			0.16				

*No data available on body size measured under competitive conditions.

SELECTION FOR DEVELOPMENT TIME

We selected for short and long development time in individuals grown under competitive conditions at the cage level (30 eggs/vial). Ten cultures were set up in Generation zero of selection and each of the selected lines and the unselected control was maintained with 10 cultures per generation. Every generation the fastest developing individuals in the fast line and the slowest developing individuals in the slow line were chosen as parents of the next generation. The number of individuals selected depended on a compromise between the achievement of the maximum selection differential and the maintenance of a minimum population size. The variance in the age of the eggs was reduced by collecting the eggs over a two-hour period. After generations of selection a competition test was set up to study the differences in competitive ability between the selected and unselected lines. The results are shown in Tables 27 and 28.

A - PRODUCTIVITY

(i) Selection for development time was effective in creating a difference in daily productivity between the selected lines in Generation 2. No control was kept at this time and in the next generation the fast line was superior in productivity to both the control and the slow line, the latter being inferior to the control. By generation 4 the superiority of the fast line over the control had vanished and both these lines were superior to the slow line in productivity.

(ii) The total productivities do not vary substantially between lines, therefore the value for daily productivity are genuine. Indeed the total productivity of the slow line is the lowest of all in Gen.3 and 4 thus reinforcing the conclusions drawn from the daily comparisons. The productivity of the fast line is superior to that of the control in Gen.4 but this may well be an artefact.

(iii) The daily and total productivities of the selected and unselected are not different in the competition test.

B - COMPETITIVE ABILITY

(i) The competitive ability of the fast line was not different from that of the unselected. The slow line had reduced competitive ability. Therefore selection for development time was effective in reducing competitive ability but not in increasing it.

(ii) An important point worth mentioning here is the lack of correlation between productivity under pure culture conditions and competitive in mixed culture. This point will be further discussed in connection with the concept and measurement of fitness.

C - BODY SIZE

The differences in body size between the selected and the unselected, measured under optimal conditions were non-significant up to Generation 4 of selection.

However significant differences in body size were found in the competition test (Gen.5). These differences were negative for the fast line and positive for the slow line. The comparisons under optimal conditions also reflected these differences.

TABLE No.27

SELECTION FOR DEVELOPMENT TIME.

GENERATION 1

DAY	1			2			3			4			5			6			7				
	Body Size			Body Size			Body Size			Body Size			Body Size			Body Size			Body Size				Body Size-Opt
	♀	W	PRD	♀	♂	PRD	♀	♂	PRD	♀	♂	PRD	♀	♂	PRD	♀	♂	PRD	♀	♂	PRD	PRD	
CONTROL	53.76	13.91	5.2	50.94	14.82	14.2	58.78	16.68	5.4	58.33	16.75	0.7	43.00	10.66	0.4							25.9	
	GENERATION 2																						
FAST	48.66	1.50	0.8	53.88	14.53	7.6	49.03	10.43	13.2	65.91	7.44	2.1	52.00	41.00	0.4	52.00	27.00	0.6				24.7	92.80
SLOW	49.50	28.00	0.3	52.42	15.10	3.9*	48.82	12.67	14.7	47.06	11.73	5.9*	65.55	9.00	1.2	56.33	7.40	0.8				26.8	89.80
	GENERATION 3																						
FAST	61.00	12.50	0.4	49.23	3.48	11.1*	44.88	3.39	8.1	56.66	15.93	2.2*	62.15	36.00	1.8	43.25	42.50	0.6	52.50	20.5	0.4	24.2	89.57
SLOW	77.00	25.50	0.4	52.33	9.53	3.9	50.33	10.84	3.1*	46.47	4.22	6.9	42.7	7.86	4.6*	52.88	14.57	2.3	43.00	25.5	0.7	21.9	89.24
CONTROL	76.50	30.50	0.4	57.38	23.42	2.5	49.55	13.65	7.0	39.15	2.97	7.9	43.53	9.72	2.6	48.40	19.12	1.3	47.42	19.0	1.0	22.7	89.23
	GENERATION 4																						
FAST	60.00		1.6	40.66	5.66	3.6	34.37	1.08	11.3	33.27	4.45	8.0	30.27	9.00	3.0	28.00	-17.50	0.8				28.3	94.08
SLOW	55.67	8.00	0.8	48.57	20.50	2.6	45.45	7.40	6.0*	37.73	5.05	8.0	37.25	-5.28	3.0	48.00	5.66	0.8				21.2	92.17
CONTROL	40.28	10.50	1.8	53.77	25.50	2.2	38.81	4.62	10.2	29.38	3.45	7.0	28.00	3.66	2.0	52.00	5.00	0.6				23.8	91.15

TABLE No.28

SELECTION 5 - DEVELOPMENT TIME (GEN.5).

	DAY 1+ 2				DAY 3				DAY 4				DAY 5			
	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD
FAST/W	+15.00		+0.67	0.80	-10.70	-11.13	+1.20	6.40	-11.25	-14.04**	-0.20	9.40	-13.86	+4.53	-5.40	9.00
SLOW/W			+1.00	0.40	-15.00	-7.00	-0.67*	1.20	-1.29	+12.92*	+0.20	9.00	-4.98	+6.15	+1.20	14.00
CONTROL/W		+16.50	+0.75	1.80	- 8.83	+1.55	+2.00	5.60	+0.57	-6.67	-1.20	11.60	-8.38	-0.66	-3.20	7.20
F RATIO			0.05	1.65			1.63	3.33			0.18	1.00			4.68*	1.35

SELECTION 5 - DEVELOPMENT TIME (GEN.5) - Cont'd.

	BODY SIZE OPTIMAL		%		TOTAL	χ^2	
	♀ WT	♀ WT	WT	W	WT+W	TOTALS	HET.
FAST/W	84.41	89.06	42	58	25.60	3.12	0.51
SLOW/W	92.33	89.06	53	47	24.60	0.39	2.02
CONTROL/W	86.77	89.06	47	53	26.20	0.61	2.33
F RATIO					0.18		

INBREEDING

Experimental plan

The inbred lines were obtained by brother-sister mating in every generation. The base populations came from our selection 2 (body size) experiment which had been selected for about 7 generations and relaxed for a good many before 10 inbred lines were constituted from each of the selected and the unselected lines.

Each generation flies were allowed to mate freely within inbreeding lines and 5 females were then collected from each line, put together with 45 other females collected from inbred lines of the same denomination (males were excluded to avoid cross breeding) and eggs were collected and cultured in competition against eggs collected from sampling the Pac white cage. Only one couple was used to propagate the inbred-line.

Inbreeding was continued for 3 generations (F = 0.5) when virgin females and males were collected from every inbred-line and mated in two groups chosen at random, within selected or unselected lines. In one group only the males were used, the females having come from the other group; the reciprocal crosses were also made and the males discarded before all the females in a given selected or unselected line were reunited and made to lay eggs. This procedure was followed in order to reduce to sero the possibility of crosses within inbred-lines. Eggs were cultured in the standard competition conditions against the Pac white competitor from the cage.

Eggs were also cultured under optimal conditions for an assessment of their maximum potential size.

INBREEDING AND CROSSING

RESULTS

A - BODY SIZE

(i) Body size was progressively reduced under optimal conditions with increasing coefficient of inbreeding. This decrease was exhibited both under optimal and competitive conditions. Under the latter the inbred control showed an inferiority in body size from generation 2 of inbreeding onwards. In generation 3, the large line, although differing in body size under optimal conditions did not show any deviation from the standard white competitor, when in competition. Thus, a line which has a markedly higher body size under optimal conditions shows no deviation at all when body size is measured under competitive conditions.

(ii) In Table 28A are expressed the deviations of the selected lines from unselected in the average reduction of body size with inbreeding. All the lines show comparable degrees of reduction in body size (measured under optimal conditions) below the non-inbred level.

TABLE 28A

	Gen. 1	Gen. 2	Gen. 3
H - CO	+0.18	+4.85	-2.40
L - CO	-0.49	+2.66	+2.76

B - COMPETITIVE ABILITY

(i) Inbreeding reduced the competitive ability of all the lines when compared with their non-inbred counterparts.

(ii) Within the inbreeding experiment the selected lines were more affected than the unselected. However these differences were only significant in the 1st generation of inbreeding and for the large line in the 2nd generation; thereafter they were non-significant. Crossing the inbred lines within selected or unselected did not alter this position.

C - PRODUCTIVITY

(i) The values for total productivity show a significant inferiority of the High line in relation to the control, in the 1st generation of inbreeding. Thereafter all such differences were eliminated. Crossing resulted in an inferiority of the small line in relation to the control.

(ii) The productivity of the early days of hatching is, in generation 1, highest for the Low line and lowest for the High line, in spite of the low productivity of the latter. The unselected were intermediate. However, in generations 2 and 3 of inbreeding the differences in early productivity vanished.

(iii) The differences in daily productivity between the inbreds and the non-inbreds are most certainly a consequence of the differences in viability.

D - VIABILITY

(i) This parameter was severely reduced in all the lines. The unselected line was affected in Generations 1 and 3, the low line in all generations and the high line in generation 3 only. Crossing brought viability back to the level exhibited by the standard competitor.

(ii) The reductions mentioned above are partially responsible for the reduction in competitive ability but they cannot account for all of it since in some instances, when viability was little affected, the reduction in competitive ability persisted. On the other hand the decrease in body size with inbreeding both under optimal and competitive conditions is indicative that growth itself was affected, i.e. "slowed down".

TABLE No.29.

INBREEDING - GENERATION 1

	DAY 1 + 2				DAY 3				DAY 4				DAY 5			
	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD
IH_1/W	+11.00	+10.90	-0.66*	2.40*	-2.21	+12.05*	-2.20	11.40	-30.00	-11.00	+0.25	1.00*	+4.50		+1.00	0.80
IL_1/W	-11.38*	-9.20*	-8.20*	12.60	-13.65*	-21.77*	-2.20	6.20		-5.00	+0.50	0.60	-15.00		+1.00	0.80
ICO_1/W	-12.61*	-3.91	-4.40	8.00	+2.23	-2.98	-0.60	12.20			+0.20	0.20			+1.25	0.40
H/W	+6.50	+9.60	-4.20	7.40*	+8.00*	+8.50	-1.00	7.80*	+5.80	+19.83*	-0.20	4.60	+1.00	+12.25	0.00	2.60
L/W	-24.26**	-16.10	-2.75	6.60	-28.57**	-16.83*	-4.00**	12.00	-28.00**	-21.40*	+0.60	3.80	-26.00		0.00	0.80
CO/W	-1.50		-2.25	2.60	+2.14	-3.53	-0.20	13.00	-5.43	-0.52		8.20		-14.00		1.60
F RATIO			5.00***	5.05***			2.32	3.27*			0.13	6.30***			0.91	1.00

INBREEDING - GENERATION 1 - cont'd

	BODY SIZE OPTIMAL		%		TOTAL	χ^2	
	♀ WT	♀ W	WT	W	WT+W	TOTALS	HET.
IH_1/W	96.86	85.78	44	56	15.60*	1.28	1.28
IL_1/W	66.28	85.78	26	74	20.20	23.77***	1.24
ICO_1/W	84.36	85.78	38	62	20.80	5.53*	2.06
H/W	100.70	85.78	42	58	22.00	2.94	1.79
L/W	70.79	85.78	36	64	23.20	8.82***	0.92
CO/W	88.38	85.78	48	52	25.00	0.20	4.70
F RATIO					4.86***		

TABLE No.30.

INBREEDING - GENERATION 2

	DAY 1 + 2				DAY 3				DAY 4				DAY 5			
	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD
IH_2/W	+5.42	+11.88*	-2.80	10.00	11.28	+19.50*	-1.50	6.00	-2.00	+27.50	0.00	1.60			+1.25	1.00
IL_2/W	-18.89***	-7.34	-5.60	12.40	+15.00		0.00	0.80	+13.00	-27.75**	+0.50	1.60			+0.33	1.00
ICO_2/W	- 0.23	+4.56	-2.40	11.20	+2.33		+1.00	2.80	-16.25**	+10.50	+0.25	1.40			+1.00	0.40
H/W	+1.43	+16.74**	0.60	1.80	+11.36*	+15.12*	-3.20	7.20	+6.63	+4.28	+1.20	10.40	+6.16		+4.00*	6.00
L/W	-20.41***	-20.20***	-0.80	4.80	-16.42*	-35.00*	-3.00	14.20		-5.00	+0.50	4.80**		-25.00	-0.33	0.60*
CO/W	-5.37	-5.12	0.25	1.40	-0.70	-6.02	-1.60	10.40	0.00	+14.66	+0.40	11.20			0.2	1.80
F RATIO			6.02***	20.00			1.20	8.50***			0.10	20.00***			4.10*	6.70***

INBREEDING - GENERATION 2

	BODY SIZE-OPT		%		TOTALS	χ^2	
	♀ WT	♀ W	WT	W	WT+W	TOTALS	HET
IH_2/W	91.64	82.30	42	58	18.40	2.13	1.19
IL_2/W	62.41	82.30	34	66	15.80	7.91**	1.80
ICO_2/W	78.42	82.30	47	53	15.80	0.31	5.32
H/W	93.25	82.30	55	45	25.4	1.33	1.08
L/W	66.21	82.30	43	57	24.4	2.09	2.08
CO/W	84.88	82.30	47	52	24.8	0.29	6.43
F RATIO					6.40***		

* Body size was estimated from the pooled data of Day 4 and Day 5+ since the numbers hatched were insufficient to allow separate estimates to be calculated.

TABLE NO.31

INBREEDING - GENERATION 3

	DAY 1 + 2				DAY 3				DAY 4				DAY 5			
	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD	♀ SIZE DIFF	♂ SIZE DIFF	C.I.	PRD
IH_3/W	+14.00		-3.00	3.80	+7.41	+2.30	-4.80	10.40	+2.16	8.64	+1.25	4.60			+1.40	1.40
IL_3/W	-26.33***	-25.57	-1.80	3.80	-27.24***	-25.06**	-4.00	10.00	-32.00*	-30.95***	-1.00	5.40		-2.50	+0.66	1.20
ICO_3/W	-6.01*	-23.00***	-2.25	4.60	-6.75*	-5.20	-6.00	10.40	-17.92*	-7.28	+0.80	4.80		+5.50	+0.66	1.20
H/W	-9.00	0.00	0.00	1.20	+5.22	+0.70	-0.40	6.40	+17.42**	+10.27*	-1.60	6.40	-0.27	+3.35	+1.00	5.80
L/W	-51.16	-0.12	2.33	3.00	-14.81	-17.38**	-2.40	10.00	-27.62**	-12.00	-0.80	5.60	-36.83**		0.00	2.40
CO/W	+20.50	+7.25	+0.20	1.80	-11.43	-6.54	-1.20	8.00	-15.00*	-6.50	-0.40	10.8	+11.35	18.00	-1.50	4.80
F RATIO			1.51	1.22			1.92	1.77			1.34	1.74			1.61	3.48*

TABLE NO.32.

INBREEDING - CROSSES BETWEEN INBRED LINES WITHIN SELECTED AND UNSELECTED LINES

	DAY 1+2		DAY 3		DAY 4		DAY 5		%		TOTAL	χ^2		BODY SIZE OPTIMAL	
	C.I	PRD	C.I.	PRD	C.I.	PRD	C.I.	PRD	WT.	W	WT+W	TOTALS	HET	♀WT	♀ W
$IH_4 \times IH_4$	-1.25	2.60	-2.80	10.00	0.00	5.20*	+1.00	2.00	42	58	19.60	2.61	0.26	96.60	90.12
$IL_4 \times IL_4$	-2.60	6.00**	-0.60	6.20	+1.00	3.40**	-0.25	1.00*	42	58	16.60*	2.03	2.56	67.12	90.12
$ICO_4 \times ICO_4$	-0.33	0.60	-1.20	6.80	0.00	10.40	-0.20	4.60	47	53	23.60	0.54	1.39	80.36	90.12
F RATIO	1.62	9.37***	1.00	2.143	0.67	8.58***	0.19	5.68*			4.24*				

COADAPTATION

When considering the problem of dispersion of a given population of Drosophila a useful approach is to consider differences in fitness between geographically distinct populations. One would expect that populations which have been kept apart for many generations may diverge genetically from each other for two main reasons. Firstly, the population size may vary widly thus introducing a source of variation due to sampling. But even if the size of the breeding population is kept relatively large there remains the second alternative - different environments to which the population must adapt. What is the meaning of the word adaptation in this context? It means maximization of fitness (productivity) under the conditions in which the population lives. If we want to make this definition applicable to a "between populations" situation the only way out is to study the difference in competitive ability between the two populations in the two corresponding environments. A superiority in both environments will mean absolute superiority of one population over the other. It is not difficult to imagine that some populations are absolutely superior to others, since populations may evolve at different rates, using different genetic solutions to respond to different selection pressures of different environments.

The idea that environment, by exerting different types of pressure on the genotypes, could generate an adjusted gene pool lead

DOBZHANSKY (1949) to coin the term "coadaptation" to designate this phenomenon. If differences between populations are present (based on linkage and interactions between genes) they dhould be expressed in terms of reduction in fitness, below the parental level, in the F2 of a cross between two populations. This test could provide an indication of the area of dispersion of a given population if other morphological or biochemical indicators failed to do so.

VETHUKIV (1954) studied the viability of several geographically distinct populations of D.pseudoobscura, D.willistoni and D.paulistorum and of the F1 and F2 hybrids (within species). He found that the F1 hybrids between different populations were superior in viability to the parental populations in all crosses of D.pseudoobscura andwillistoni but present in only one cross of D.paulistorum. However this superiority broke down in the F2 giving individuals which were on average inferior to both parents, this inferiority being more pronounced in pseudoobscura and willistoni than in paulistorum. VETHUKIV concludes, in favour of DOBZHANSKY's ideal that the genotypes of geographic populations are integrated systems of genetic elements which arose during evolution through the action of natural selection. ANDERSON (1968) studying body size in D.pseudoobscura reached roughly the same conclusions. On the other hand MCFARQUHAR and ROBERTSON (1963) studying coadaptation

for body size in Scottish populations of D. subobscura found no evidence for it. More recently ALAN ROBERTSON and KNIGHT (1970) unpublished) looking at sternopleural bristle number in populations of D.subobscura picked in Scotland but in a different direction from the one used by MCFARQUHAR and ROBERTSON (1963) also found no evidence for coadaptation suggesting that the Scottish populations of D.subobscura constitute one large breeding unit. The same type of result was found by LOPEZ-FANJUL (personal communication) when analysing crosses between the KADUNA and PACIFIC populations of D.melanogaster.

The criticism to be made at this stage is of a technical nature: the conditions under which the expected breakdown of fitness was observed were probably not the suitable ones:

EXPERIMENTAL

As we said in the introduction the evidence for coadaptation in Drosophila is not constant between different species. In orderto check the existence of coadaptation in two geographic populations of D.melanogaster, we studied the F1 and the F2 of a cross between the PACIFIC (Pac) and the KADUNA (NK) populations. The standard competitors used in this experiment were the Pacific white-eye (Pac w) and the Kaduna white-eye populations, both of which arose by backcrossing

repeatedly a white eye mutant into the wild-type stock and then propagating these populations in cages. Pac w had been kept in the cage for 14 months at the beginning of this experiment, wherease Kaduna w (WK2) had been run for about 10 years.

The results expected on the basis of the null hypothesis of no coadaptation in the gene pools of the populations involved are an F2 which is not inferior in fitness to either of the parents, in other words, there will be no "breakdown of fitness".

The experimental plan was as follows:

P ♀ Pac x ♂ NK

♀ NK x ♀ Pac

F1 eggs from the above crosses were cultivated in competition against each of the white populations (5 replicates each) in fixed proportion (0.5:0.5), following the normal procedure. The controls were represented by competition within populations between the wild-type and the white variants.

F2 In this generation individuals from both F1s were allowed to mix and mate freely; eggs were collected and cultivated under the same conditions of the F1, in competition against the two white populations. The same controls were used; in addition competition was studied between wild type populations of one origin against the white-eye population of the other provenience.

The results of these experiments are presented in Tables 33 and 34. The main conclusions are:

RESULTS:

A - BODY SIZE

(i) The analysis of body size measured underoptimal conditions indicates that there are differences in body size between the Pacific and the Kaduna populations, the latter being smaller than the former.

(ii) The analysis of the differences of body size measured under competitive conditions (within days) shows that in the F1 both reciprocal crosses, the Pac and Kaduna wild type and the Pac white populations do not differ in average body size. The same cannot be said about the Kaduna white eye population which shown an appreciable reduction of body size, when compared with the above mentioned populations.

B - COMPETITIVE ABILITY

(i) This parameter also shows substantial variation within days. This is a consequence of the poor competitive ability of the WK2 stock.

(ii) The competitive ability of the two reciprocal crosses are similar although this similarity is disguised by the poor viability of the ♀ NK x ♂ Pac cross. However a calculation of a competitive index corrected for viability reveals immediately the equality in competitive ability.

(iii) The competitive ability of the two reciprocal crosses does not differ significantly from that of the two parent populations.

C - PRODUCTIVITY

(i) Productivity showed marked variation within days. This variation is attributed to two factors: the low competitive ability of the WK2 flies most certainly due to a reduction in feeding rate and the low viability of the cross ♀ NK x ♂ Pac.

(ii) Total productivity also showed significant variation between types of cultures. Again this is due to low viability of the cross mentioned above.

D - VIABILITY

This parameter is significantly reduced in the ♀ NK x ♂ cross. This effect is independent of the conditions of the culture since it is also shown under optimal conditions.

COADAPTATION

F2

A- BODY SIZE

(i) The values for body size of the F2's measured under OPTIMAL are the same for the progeny of both reciprocal crosses.

(ii) When body size is estimated from competition experiments, no difference can be observed between the F2's and the Pac white. The same applies to differences between the Pac WT, Pac W and the Kaduna WT population. Differences between the F2 and the WK 2 wre extremely significant in the same way as the differences between this population and the Pac WT and the Kaduna WT.

B - COMPETITIVE ABILITY

(i) The competitive index shows significant variation in Day 1 + 2 due to the reduced competitive ability of the WK2 population component with the Pac white population.

(ii) The competitive ability of the F2 does not differ from that of the two parent populations.

C - PRODUCTIVITY

No significant variation was observed in this parameter.

D - VIABILITY

No significant differences in viability were found.

CONCLUSIONS FROM THE COADAPTATION EXPERIMENT

(i) Both the F1 and F2 of the cross between Pacific and Kaduna showed little deviation in body size from that of the parents.

(ii) The 2 Pacific populations and the Kaduna WT show similar body size measured under competitive conditions. The Kaduna WT shows a slight inferiority in body size in relation to the Pacific populations, this inferiority is observed under optimal and competitive conditions.

(iii) The Kaduna white population shows a marked inferiority of body size measured under competitive conditions in relation to the Pac, WT, NK, F1 and F2 competitors. This reduction in body size is in all ways comparable to the one observed in lines selected for small body size. The difference in body size between NK and WK2 measured under optimal conditions is not significant.

(iv) The competitive ability of the F1 and the F2 does not differ from that of the parent populations when measured against the two white-eyed populations.

(v) There is a maternal effect on viability, the eggs possessing a NK cytoplasm being less viable than thos possessing the alternative cytoplasm.

(vi) All this evidence taken jointly suggests that crossing the two populations had no effect on body size and on competitive ability, thus suggesting that the two WT populations have a similar array of genes controlling growth. In other words there is no coadaptation as far as these genes are concerned. The fact that the WK2 population has a reduced body size under comeptitive conditions suggests that the introduction of the white gene into the Kaduna background had different effects from that of introducing the white gene into the Pacific background; i.e. effects that interfered with the nature of growth itself. The fact that the white gene of the WK2 population was derived from a "white singed" (ALAN ROBERTSON, personal communication) stock raises the interesting possibility that the cause of the similarity in growth behaviour between this line and lines selected for small body size is located in the chromosomal region occupied by the "white singed" complex.

TABLE 33

COADAPTATION. F_1 PACIFIC x KADUNA.

DAY	1+2				3				4			
	SIZE DIFF.				SIZE DIFF.				SIZE DIFF.			
	♀	W	C.I.	PRD	♀	♂	C.I.	PRD	♀	♂	C.I.	PRD
♀ Pac) ♂ NK) PacW	+4.20	+0.70	+3.00	8.2	+2.20	+0.29	-2.00	18.0			-2.75	2.6
♀ Pac) ♂ NK) WK2	+13.46	+30.00**	+9.00	10.2	+19.82***	+38.16***	-1.60	11.6			-3.80	4.6
♀ NK) ♂ Pac) PacW	+1.40	+7.13	+2.20	13.4	-4.46	-7.93	-3.00	11.4			-1.00	0.2
♀ NK) ♂ Pac) WK2	+11.56**	+19.82***	+2.80	12.0	+17.16*	+19.50**	-3.25	5.8			-1.80	1.8
Pac WT/W	-6.13	-2.46	+3.00	11.4	+2.27	-7.04	-4.60	12.2			-0.67	2.0
KAD NK/WK2	+14.00	+0.30	+2.20	4.6	+20.73***	+18.06***	+3.60	16.4	+15.66*	+21.27	-3.60	5.6
			2.11	3.11*			2.84*	2.85*			1.18	5.60***

In days 4 and 5 the number of individuals hatched was not sufficient to allow the calculation of all the differences in body size.

COADAPTATION F_1 PACIFIC x KADUNA - Cont'd.

DAY 5

	SIZE DIFF ♀	SIZE DIFF ♂	C.I.	PRD	TOTAL PRD	% WT	% W	χ^2 TOTALS	χ^2 HET.	BODY SIZE - OPTIMAL ♀WT	BODY SIZE - OPTIMAL ♀W
♀ Pac) ♂ NK:) PacW			+1.00	0.6	29.4	49	51	0.06	0.19	85.93	84.44
♀ Pac) ♂ NK) WK2			-1.00	1.4	27.8	55	45	1.21	3.38	85.93	78.99
♀ NK) ♂ Pac) PacW			-1.50	0.6	25.6	48	52	0.28	0.90	90.21	84.44
♀ NK) ♂ Pac) WK2			-0.00	0.4	20.0	46	54	0.64	10.58*	90.21	79.99
Pac WT/W			+2.00	0.4	26.8	43	57	2.41	1.19	83.80	84.44
KAD NK/WK2			-1.34	0.8	27.4	53	47	0.35	2.29	81.47	78.99
			7.05***	1.35	4.56**						

TABLE 34

COADAPTATION. F2 PACIFICxKADUNA

DAY	1+2				3				4				5				TOTAL
	SIZE DIFF ♀	SIZE DIFF ♂	C.I.	PRD	SIZE DIFF ♀	SIZE DIFF ♂	C.I.	PRD	SIZE DIFF ♀	SIZE DIFF ♂	C.I.	PRD	SIZE DIFF ♀	SIZE DIFF ♂	C.I.	PRD	PRD
F2/PacW	-3.37	+10.5	-0.75	5.4	-0.10	-5.88	+2.00	9.6	-1.28	+1.01	-1.00	7.4	+13.85	-1.35	-1.40	3.0	25.4
F2/WK2	+25.75*	+19.62**	+2.33	3.4	+23.08***	+11.00*	+3.60	10.8	+28.83***	+19.72***	-1.60	10.8	+38.08***	+0.44	-2.00	3.2	28.2
Pac WT/W	+14.77	+6.57	+0.50	8.0	+3.98	-1.72	-0.20	9.0	+2.60	+4.60	-1.25	8.2	-3.50		+0.67	1.8	27.0
KAD NK/WK2	+7.02	+18.30*	+0.80	5.2	+4.92	+16.49	+0.60	10.2	+4.95	+23.14*	-0.25	5.4		-23.07*	-1.00	2.4	23.2
Pac WT/ WK2	+48.03*	+26.08**	+6.50	7.2	+32.64***	+24.62***	-0.80	7.2	+21.00*	+22.88*	-0.20	6.2			-2.75	2.2	22.8
NK/PacW	-7.71	+9.33	-0.50	6.8	-13.62	+0.22	-1.40	7.0	-19.03*		+0.25	3.0	-8.02		-2.00	3.6	20.4
F RATIO			3.87*	0.5			1.18	0.82			0.26	1.58			0.61	0.79	2.13

COADAPTATION, F2 PACIFIC x KADUNA - contd

	%		χ^2		BODY SIZE-OPTIMAL	
	WT	W	TOTALS	HET	♀WT	♀W
F2/PacW	48	52	0.19	1.33	92.54	87.00
F2/WK2	54	46	0.86	2.85	92.54	82.40
Pac WT/W	49	51	0.07	3.13	88.10	87.00
KAD NK/WK2	51	49	0.03	5.32	84.23	82.40
Pac WT/WK2	54	46	0.87	7.60	88.10	82.40
NK/Pac W	43	57	1.92	3.91	84.23	87.00

EXPERIMENTS ON EGG PRODUCTION

In these experiments we studied the effects of varying the food input in the adults and in the larvae of Drosophila on egg production. In the two experiments described the selected lines used and the unselected population were drawn from the corresponding lines of the sel 2 experiments.

VARIATION IN THE FEEDING PERIODS

This experiment was designed to test the capacity of oviposition of the selected and unselected lines for body size, when different regimes of feeding were given to the adult flies. The egg production of the flies was measured for the first 4 days of adult life at 4 different levels of feeding - 0, 1, 5 and 24 hrs. a day in contact with a rich suspension of live yeast.

The results of this experiment are shown in Table No.35.

(i) The unselected line has a superior egg production in the first or first two days of oviposition. This superiority, however, vanishes by the 3rd or 4th day of life, time when all the lines have comparable values for egg production.

(ii) The egg production of the flies is very sensitive to food shortage. The time taken for the conversion of the food ingested into eggs is less than one day as indicated by the differences between levels of feeding in the egg production of the 1st day.

(iii) The large line has a lower rate of increase in egg production than any of the other two lines. The comparison of the 5 hr level of feeding with the 24 hr level reveals that the unselected flies can "make the most" in terms of egg production when faced with a food restriction.

(iv) When no food is given to the flies the unselected show a clear superiority in the first two days of life. It is possible that this superiority is consequent to a larger amount of "residual" eggs.

VARIATION IN THE LEVELS OF CROWDING

In this experiment eggs from the lines selected for large and small body size and the unselected control were cultured under different conditions: optimal and competitive (10,30 and 40 eggs/vial). Egg production was measured by feeding the adults a rich suspension of yeast, 24 hrs. a day. The results of this experiment are summarised in Table 36.

(i) Three estimates of egg production were calculated. When the flies were grown under optimal or competitive conditions at 30 and 40 eggs/vial, the three estimates give a consistent picture of egg production. The same does not happen in flies grown under competitive conditions at 10 eggs/vial since the superiority of the unselected over both selected lines in Day 1 and Day 1 + 2 is eliminated in relation to the large line when the egg production of Days 5 to 8 is considered.

(ii) The unselected is superior to both selected lines under optimal conditions. At the levels of 30/ and 40/egss vial no difference in egg production is detectable between selected and unselected lines.
(iii) Although the flies grown under optimal and those grown under competitive conditions at 10 eggs/vial have the same adult body size their egg production in the 1st day is remarkably different. This could be due to the reduced amount of biomass available for the fabrication of "residual" eggs in the flies grown under competitive. That competitive conditions were effective in affecting the speed of growth is indicated by the increased development time of these flies were compared with these grown under optimal.

CONCLUSIONS

These results suggest that when flies are grown under cage conditions or similar ones the egg production of the first few days is correlated with that of the peak period of egg-laying (5th-8th day of life). Moreover differences in egg production are not likely to be important as components of fitness under these circumstances, since the two selected lines and the unselected showed comparable levels of egg production at all days.

TABLE 35

EGG PRODUCTION OF LINES SELECTED FOR LARGE AND SMALL BODY SIZE AND UNSELECTED. DIFFERENT FEEDING PERIODS.

DAY	1	2	3	4
NO FOOD				
H	4.8	2.9	16.4	2.5
L	2.7	2.6	12.5	2.0
CO	7.4	11.7	7.0	1.2
1 hr/FOOD/DAY				
H	6.5	22.4	17.3	17.8
L	11.1	27.0	20.4	18.1
CO	10.6	29.0	12.0	12.4
5 hrs FOOD/DAY				
H	4.3	38.2	30.9	42.3
L	8.4	32.8	25.7	35.3
CO	25.1	28.6	32.8	37.7
24 hrs/FOOD/DAY				
H	8.6	71.9	97.3	100.1
L	15.8	83.9	94.6	102.2
CO	28.5	87.7	85.7	103.8

TABLE 36

EGG PRODUCTION OF LINES SELECTED AND UNSELECTED FOR BODY SIZE

Conditions of Larval Growth	Line	Day 1	Days 1 + 2	Days 5+6+7+8
OPTIMAL	L	14.1	49.87	73.16
	H	24.5	58.10	86.13
	CO	31.0	63.15	94.17
COMPETITIVE (10 eggs/vial)	L	7.3	46.9	73.77
	H	4.8	44.7	94.32
	CO	16.7	54.8	85.47
COMPETITIVE "cage-level" (30 eggs/vial)	L	8.9	42.30	69.67
	H	8.6	38.85	78.30
	CO	6.6	41.6	70.97
COMPETITIVE (40 eggs/vial)	L	6.3	35.5	67.97
	H	8.8	37.35	67.45
	CO	6.4	36.35	71.00

INTERSPECIFIC COMPETITION

As we have seen before, our model of competition in the way it is described here, can only be applied to colonizing species. When we decide to study interspecific competition we must be sure that there is some ecological relevance in studying competition between any two species chosen, especially that their niches can overlap. Examples of non-overlapping would refer to two types of food or different temperature ranges which would automatically exclude one of the species. Also, we need to know all the fitness components relevant to the ecological situation in which the species are competing. Even if we manage to identify these conditions the fact remains that competition, studied in this way, is not only a very tedious job but, since the results are restricted to the two particular competing populations, we are unable to make generalizations to other populations and species. The only way to achieve such generalization is through an understanding of the physiology of competition, in the same way we have attempted for the intraspecific situations. We were able to see how much care we had to use in choosing the right competitor when studying stabilising selection and frequency dependant selection: under the conditions used the key to the identification of variation in such parameters as critical size, efficiency of food conversion and appetite lies in the similarity in genotype between the populations studied. Widely different populations may exhibit similar competitive abilities based on quite different growth patterns, as we have pointed out earlier.

Another point we must consider carefully is the consequences of competition under different regimes of colonization, since selection coefficients will be very much dependent on this, as we saw in connection with our discussion of intraspecific, frequency-dependent selection. The same applies here; if we imagine that the rate of appearance of new niches is subject to some fluctuation, regular (seasonal) or irregular it is clear that the advantages of each species will also fluctuate following some kind of function. This will be discussed later in greater detail.

1) Competition between pseudoobscura and willistoni

AYALA (1971) studied competition between these two species, in his "serial-transfer" system (STS) and found that a frequency dependent selection mechanism was operative, keeping the frequencies of the two populations at a given equilibrium value. He suggests that this mechanism must operate during the larval stage as proved by the differences in productivity between cultures with different initial proportions of each species and the lack of differences in survival of the adult flies produced by these cultures. Moreover he suggests that the advantage shown by willistoni during the larval stage is compensated by the greater longevity of pseudoobscura in the adult stage. Since AYALA is trying to extrapolate from this data to the possible coexistence of the two species in the same niche under natural conditions we must consider his experiment in greater detail.

We may consider first the ecological relevance of STS: this system consists in the transfer of all the flies from a set of 5 bottles to a new one in the beginning of every week, discarding the oldest bottle in the set thus keeping a constant number of bottles. The test was started with a fixed number of adult individuals in varying properties all put together in one bottle. At the end of the week the survivors of this bottle were shaken to a new bottle and so on, until the 6th bottle was started on the date on which the 1st bottle was discarded. Therefore all the new flies hatched in each of the five bottles in the period of five weeks were collected weekly and mixed with the survivors from the initial parent. This mixture constitutes the population studied by AYALA. It does not require much expertise to see that development time is completely eliminated as a component of fitness in this system, both within bottles (differences within a week are reduced to zero) and between bottles since different bottles willhave necessarily different species proportions (otherwise there would be no frequency-dependent selection and therefore different productivities and different selection coefficients for each species: mixing 5 different bottles will undoubtedly eliminate many of these differences.

On the other hand it is perfectly clear that the serial transfer system does not correspond ecologically to the situation in which there is a positive rate of appearance of new niches for colonization; when this rate is constant, provided the appearance of new niches is randomly

distributed in time the fastest developing species would maintain its advantage. However when the rate of appearance of new niches is declining, the advantage of willistoni in terms of development time will be reduced to zero and the longevity of pseudoobscura will play an increasingly important part.

AYALA's claim that competition under STS involves all stages of life and is fully comprehensive has to be set beside the impossibility of predicting the outcome of competition between other species or other populations of the same species; in other words his experiments do not allow generalization; he couldn't even account for the differences between the two populations of willistoni which he used. This does not surprise us since no attempt was made to identify the physiological factors responsible for differences in competitive ability and productivity. AYALA's work also lacks a survey of the differences in the classical components of fitness measured under optimal conditions: egg production, body size and development time which can give us an indication about the growth characteristics of the species involved.

We will attempt to see what inferences can be drawn from AYALA's data about our physiological parameters and use them in a simulation process. But let us look first at the main conclusions from AYALA's experiments:

a) D.willistoni develops faster than D. pseudoobscura. The magnitude of this difference is a function of the degree of crowding in pure cultures (Table 2, AYALA, 1971) and of the species proportions in mixed cultures (Table 1 AYALA). In mixed cultures this difference can be expressed in terms of a

competitive index which is a weighted difference (C.I. = $\frac{\text{w adults per culture}}{\text{initial no. of w adults}}$ - $\frac{\text{p adults produced per culture}}{\text{initial no. of p adults}}$).

Proportion of W	M 11			RP3		
	Productivity	C.I.	W/P	PRD	C.I.	W/P
0.20	350	+0.725	1.13	293	+0.346	0.637
0.50	498	+0.264	1.72	417	+0.327	1.56
0.80	669	-0.214	1.98	556	-0.167	3.02

M11 and RP3 are the two populations of willistoni used. Productivity is the total number of individuals hatched in the cultures per week. W/P is the ratio of the number of individuals of each species hatched per week.

We can see that, within the weekly intervals considered, and assuming necessarily that egg production was not different for both species, the relative advantage of w is negatively correlated with its proportion. However the ratio of absolute numbers of each species, hatched per week is generally greater than one even when w is at a low proportion (with the exception of the 200 RP3 w/800 p level).

b) The productivity of the cultures is positively correlated with the proportion of willistoni in mixed cultures. In pure cultures and within the range of crowding studied by AYALA, the maximum values for w are 768 and 559 (M11 and RP3 respectively) at a crowding level of 1000, and of 306 for pseudoobscura at a crowding level of 200 adults. The fact that productivity does not show a lower plateau within the range of crowding studied allows us

draw no conclusions about the egg production characteristics of the two species, in other words we will not be able to say with absolute certainty whether the differences in productivity at a given level of crowding are due to variations in egg production or in the intensity of intraspecies competition; however the fact that the productivity of p in mixed cultures does not vary, in spite of wide variation in the initial numbers of this species, points to the conclusion that egg production is not the restrictive factor.

c) The longevity of D.pseudoobscura is greater than that of D.willistoni, generating a correlation between development time and longevity. There is no effect of crowding or species proportion on survival of adults.

What conclusions can we draw from these results?

1) Since body size in willistoni is smaller than in pseudoobscura we can reasonably assume that they consume less food than pseudoobscura. This alone would lead us to expect differences in productivity of cultures with different proportions of the two species, but it fails to explain:

2) the faster development rate of willistoni. Given the conclusion of no.1, development period must be shorter in w than in p. In other words the component critical size duration of 2nd period must be smaller in w than in p. Alternatively,

3) pseudoobscura could have the same critical size as w but a lower efficiency of food conversion such that the product of appetite and efficiency is more reduced in p.

We shall simulate three possible situations in our predator-prey system and see how the results fit AYALA's data.

I - p with higher feeding rate, higher critical size but the same efficiency as w.

II - p with higher feeding rate, lower efficiency but thesame critical size as w.

III - p with the same feeding rate, same efficiency but a higher critical size than w.

The results of this simulation are summarised in Table 37. As we can see from the examination of Table 37. the only combinations of the different physiological parameters capable of fitting AYALA's data are the ones where $R1 < R2$ with feeding rates negatively correlated with efficiencies of food conversion. However, even this solution has its subtleties: a delicate balance must be achieved between the difference in R between the two competitors and the difference in critical size. Critical size can be a neutral circumstance (as far as the type of result is concerned) as can be observed from the comparison of 5 with 6 where an increase in critical size of p made no alteration in the pattern of relations between PRD and CI. However, when we compare F with 8 we can see how this pattern can be altered just by altering critical size. Therefore, our predictions for the differences in physiology between willistoni and pseudoobscura are:

TABLE NO.37.

SIMULATION OF COMPETITION BETWEEN D.WILLISTONI AND D.PSEUDOOBSCURA

$R_1 = R_2$	CSW = Csp	(C1 = 0.50) (C2 = 0.75)	PRD ↑	C.I. = K
	CSW < Csp	(C1 = 0.50) (C2 = 0.55)	PRD ↑	C.I. ↑
	CSW < Csp	(C1 = 0.5) (C2 = 0.5)	PRD = K	C.I. ↑
$R_1 > R_2$	$\frac{1}{2}$CSP < CSW < CSP	(C1 = 0.50) (C2 = 0.75)	PRD ↑	C.I. ↑
	CSW = CSP	(C1 = 0.50) (C2 = 0.75)	PRD ↑	C.I. ↑
$R_1 < R_2$	CSW = CSP	(C1 = 0.50) (C2 = 0.75)	PRD ↑	C.I. ↓
	$\frac{CSP}{2}$ < CSW < CSP	(C1 = 0.50) (C2 = 0.75)	PRD ↑	C.I. ↓
	CSW = $\frac{1}{2}$CSP	(C1 = 0.50) (C2 = 0.75)	PRD ↑	C.I. ↑
	CSW = $\frac{1}{2}$CSP (R_1 R_2)	(C1 = 0.50) (C2 = 0.75)	PRD ↑	C.I. ↓

R_1 and R_2 are the growth rates of willistoni and pseudoobscura respectively. CS stands for Critical Size, C.I. and PRD for Competitive Index and Productivity respectively. C1 and C2 are the feeding rates of w and p and $\frac{R1}{C1}$ and $\frac{R2}{C2}$ their efficiencies of food conversion.

a) Higher feeding rate for p than for w

b) Higher efficiency for w than for p

c) The product of efficiency and feeding rate (growth rate) is larger for p than for w

d) Critical size (an indication of adult body size) could be larger although this is not always a necessary condition as we saw before. However, it is likely to be true given the large differences in adult body size observable between willistoni and pseudoobscura.

Having looked at the effects of one generation of competition on the proportions of the two species we must now pay attention to the outcome of competition when different colonization processes are at work. In short we will look at the following situations:

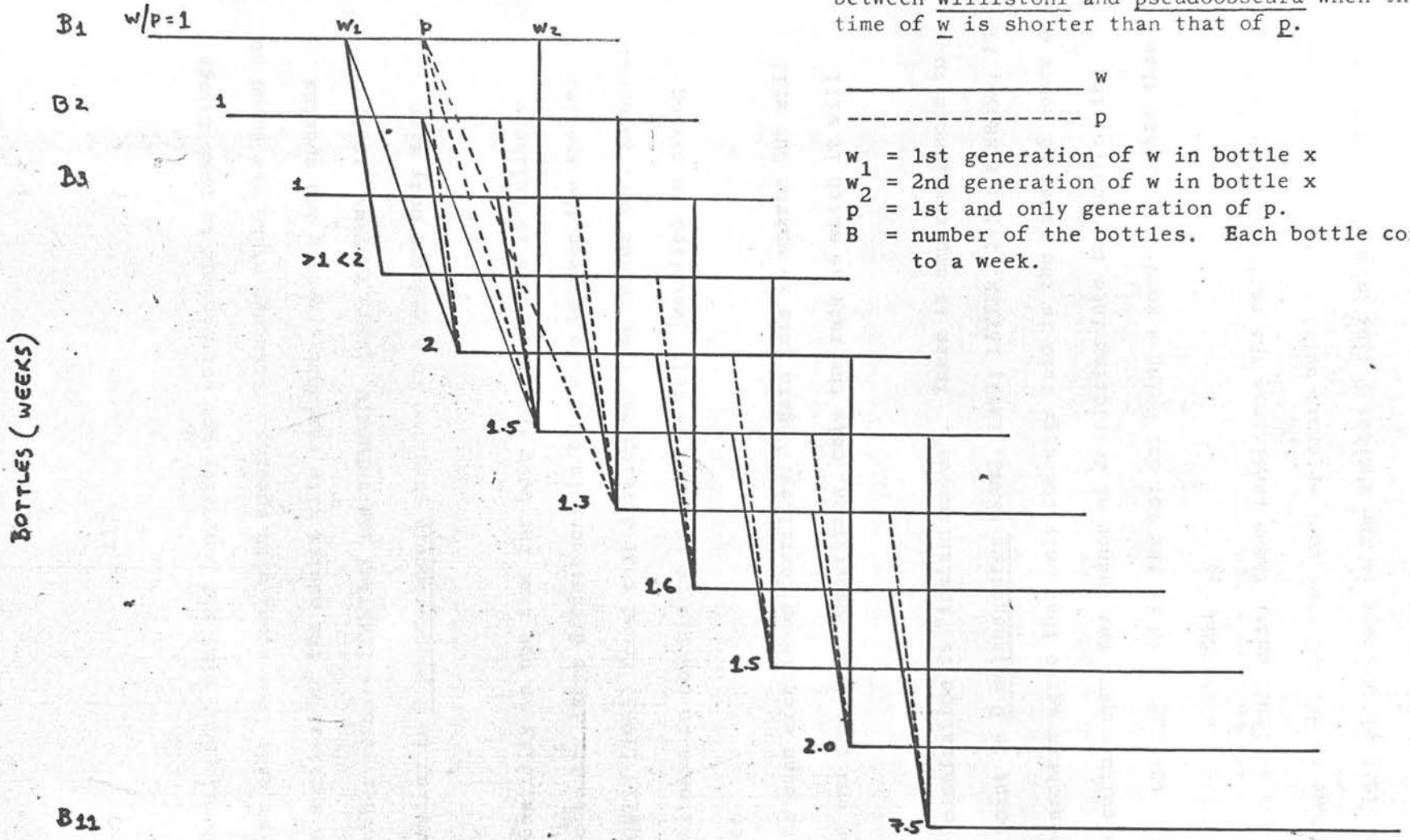
a) When the importance of development time is almost reduced to zero but that of longevity kept as a component of fitness.

b) When both development time and longevity are taken into account.

We will study the changes in species frequency in the 1st case by using a very elementary method of drawing graphs and adding the frequencies from the 5 bottles composing STS, at the beginning of a new graph (or week). The assumptions in this study which can undoubtedly be improved through the use of suitable algebra and computer programming, are:

FIG. 3

Simulation of competition under a serial-transfer system between willistoni and pseudoobscura when the development time of w is shorter than that of p.



———— w

---------- p

w_1 = 1st generation of w in bottle x
w_2 = 2nd generation of w in bottle x
p = 1st and only generation of p.
B = number of the bottles. Each bottle corresponds to a week.

1) Development time and longevity are correlated; to make things easier for us we made them equal with species. Although AYALA has found no differences in survival of the adults with variable crowding and species proportions, other authors (TANTAWY and VETHUKIV, 1960; TANTAWY, 1961) found that crowding in D.pseudoobscura resulted in a reduced body size and longevity.

2) Fertility is the same for both species. This is unlikely to be true due to the large differences in body size between the species but since LEWONTIN (1965) found that development time is the most important component of fitness in colonizing species, we felt justified in making this assumption.

3) No oage effects on fertility. Again this is untrue but will not affect the end result of competition, only the rate at which it will be achieved.

4) Colonization is "instantaneous". There is ample evidence to support this point in D.melanogaster (SANG, 1949; LATTER, 1958; KINROSS, 1969). All these researchers agree that only the eggs laid in the first 48 hours of the life of a culture have any chance of developing into the adults, the probability for the eggs laid in the 1st day being a good deal higher than that for those laid on the 2nd day.

(Fig.3)

We can see that under these conditions the ratio w/p goes up to 2 then comes down to 4/3 and then goes up again until it eliminates p. The reason for the initial increase is the shorter D time of w. The reason for

the subsequent decrease is due to the appearance of the offspring of P, from bottles started with the initial proportion 1:1 and this counteracts the increase in w/p. Once this factor is eliminated the frequency of p in the cultures will progressively decrease.

If we make the difference in development time between the two species somewhat smaller we may be able to reach a situation of coexistence of the two species. This effect would be further reinforced by turning our deterministic model into a stochastic one where there would be a certain degree of overlapping of the distributions of development time of the two populations with the consequence of delaying the elimination of the slow developing species. A point worth stressing at this stage concerns the variance of the ratio willistoni/pseudoobscura between the 5 bottles which provide the founder individuals for a new bottle each week. This variance, which is caused both by the initial ratio in each bottle and the age of the bottles, will generate considerable oscillation of the ratio of the two species with time and is another indication that the equilibrium claimed by AYALA is nothing but a technical artefact. Recently, BOROWSKY (1971) made some comments on another paper by AYALA (1969) where competition between D.serrata and D.pseudoobscura was studied. BOROWSKY pointed out that the oscillations of the frequencies of each species in time were not randomly distributed, therefore no time equilibrium existed; he suggested that this effect might have been a consequence of temperature fluctuations.

If the situation under discussion is similar to the one which involves D.pseudoobscura and willistoni it is just possible that another artificial situation has been created by the use of STS and that the non-random fluctuations in species ratios are due to variance between bottles caused by differences in intial ratios as well as the age of bottles. If this is true, then the evidence presented by AYALA is not only ecologically irrelevant, but does not spread any light on the problem of the coexistence of competing species.

If we now look at our 2nd situation, where development time and longevity play their full part in determining the outcome of competition, we can see immediately that as long as niches are available for colonization between the hatching of the faster growing species and that of the slower one, the latter will soon be eliminated. If however the fast-growing species begins the colonization period at low frequency it may be possible that it will increase its advantage up to mid-season, when the rate of appearance of new niches begins to decline and the individuals with greater longevity will be at an advantage which will give them the superiority in numbers they need to be able to survive from the beginning to the middle of the new colonizing season. Therefore in this model coexistence between competing species which show large differences in competitive ability will be very much a function of the environment, but a natural one in this case instead of the artificial ones, like STS.

The next evidence to be considered is that provided by BARKER and PODGER (1970). These authors performed an extensive series of experiments on competition between D.melanogaster and D.simulans in which the relevant parameters of fitness were observed and recorded under various conditions of crowding and different proportions of each species. We must make clear at this stage that BARKER and PODGER used a dead yeast system (DYS) throughout their experiments; as we stressed before, although competition under DYS can provide a good estimate of competitive ability it does disregard the fact that natural systems are always live-yeast ones (LYS) and that the individuals which die under DYS would probably not die under LYS, only their development would be delayed. This fact may or may not be relevant: only a detailed consideration of the ecological situation at a given time will allow us to choose one way or the other. The argument put forward by BARKER and PODGER, that at high levels of crowding live-yeast cultures would be yeast-free will have some meaning only when cannibalism provides all the food supply needed by the growing larvae, in other words when the medium is exhausted.

The principle conclusions reached by these authors were as follows:

a) The results were not homogeneous at different times for the same experimental design and stocks.

b) No predictions could be made of the results of competition in mixed cultures from the results of single-species cultures.

c) At low crowding density the developmental period of simulans was significantly shorter than that of melanogaster with constant body weight and viability. BARKER and PODGER conclude from this fact that simulans has a higher growth rate and this led them to predict that simulans would be at an advantage in competition at higher densities. This prediction held true up to a certain point (density 16) accompanied by a greater size for simulans and an invariable viability. As density was further increased the prediction failed and the competitive advantage turned to be melanogaster's which exhibited higher viability from density 64, heavier absolute body weight from density 128 and equal development time from density 256 (the maximum density being 512). So much for pure cultures; in mixed cultures, within densities, a decrease in the frequency of simulans was followed by a decrease in developmental time and an increase in body size and viability. BARKER and PODGER suggest on the basis of these results that melanogaster may have a higher critical weight and/or a higher food requirement.

The same type of result was found by MILLER (1964) when studying competition between D.melanogaster and D.simulans, using a Kalmus system. However MILLER says he was able to predict the outcome of mixed cultures from the results of single-species cultures; he found that melanogaster tolerated high levels of crowding better than simulans therefore it should have an advantage of simulans at high levels of crowding.

EL-HELW and ALI (1969) also studied competition between these two species of Drosophila when fed with two types of yeast. They found that

both species thrived better in medium supplemented with Saccharomyces than with Schyzosaccharomyces; they attributed this effect to the different constituents, nutrients or inhibitors of each of these two types of yeast. With Saccharomyces, increasing density reduces the proportion of simulans in agreement with the results of the previous authors; in Schyzosaccharomyces the reverse happens.

In the face of the results obtained by these authors we propose that:

a) the frequency-dependent effect (variation in productivity and relative fitness of the species) within densities points in the direction of a slow feeding melanogaster competing with a faster feeding simulans.

b) these differences in feeding rate are probably correlated with differences in critical size, simulans having a larger relative critical size as one can guess from the greater tolerance of by melanogaster to high levels of crowding. Alternatively they may have the same critical size but simulans would possess a lower efficiency of food conversion.

c) it is likely that the two species do not differ in the duration of the post-critical period if their critical sizes are the same, but if simulans has a higher critical size with the same growth rate as melanogaster, then its post-critical period will be proportionally reduced.

We will now attempt to simulate competition between melanogaster and simulans under two sets of circumstances:

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We will now attempt to simulate competition between melanogaster and simulans under two sets of circumstances:

I - According to BARKER and PODGER's interpretation of the data

II - Our own interpretation.

If we estimate a competitive index (difference between "realized biomass") and the total productivity from BARKER and PODGER's **FIG. 5**, we will be able to present their data as follows:

CROWDING \ Ratio M/S		75/25 C.I.	75/25 PRD	50/50 C.I.	50/50 PRD	25/75 C.I.	25/75 PRD
4.	C.I.↓ PRD = K	+0.16	3.5	0.00	4	-0.16	3.5
16.	C.I.↓ PRD = K	+0.125	11.5	0.00	12	-0.16	12
64.	C.I.↓ PRD = K	+0.18	43.0	+0.11	39.5	+0.06	42.5
128.	C.I.↓ PRD ↑	+0.23	54.0	+0.11	62.0	+0.04	67.5
256	C.I.↓ PRD = K	+0.20	42	+0.078	35	-0.02	44.5
512	C.I.↓ PRD ↑	+0.036	10.5	+0.013	6.5	-0.018	7

BARKER and PODGER suggested that their results could be explained by assigning to D.melanogaster a higher food requirement and/or higher critical weight. We examined these possibilities by simulating in a computer, competition between D.melanogaster and D.simulans using the self-simulation system described elsewhere (see Table 38).

a) HIGHER CRITICAL SIZE OF MELANOGASTER

CM = CS = 0.50

RM = RS = C x 4

CRITICAL SIZE M = 0.750

CRITICAL SIZE S = 0.684

Under these conditions total productivity, C.I. and realized biomass of each competitor remain unchanged with varying proportions of each component.

b) LOWER EFFICIENCY OF MELANOGASTER

CM = 0.50

CS = 0.50

RM = CM x 3.6

RS = CS x 4

CRITICAL SIZE M = CRITICAL SIZE S

As frequency of simulans decreases, total productivity increases C.I. decreases and the realized biomass of both species decreases.

c) HIGHER FEEDING RATE OF MELANOGASTER

CM = 0.50

CS = 0.48

RM = CM x 4

RS = CS x 4

CRITICAL SIZE M = CRITICAL SIZE S

Decreasing frequency of simulans leads to a very mild increase of productivity down to a frequency of 0.5 and a comparable decrease thereafter; C.I. decreases and the realized biomass of both species does likewise.

As we can see, the outcome of competition in our system does not fit the predictions made by BARKER and PODGER. Therefore we decided to test out our hypothesis on the situation by proposing

d) SLOWER FEEDING MELANOGASTER

CM = 0.48

CS = 0.50

RM = CM x 4

RS = CS x 4

EQUAL CRITICAL SIZE

This is the same situation as in c) but in reverse. A decrease in the proportion of simulans has almost no effect on total productivity, but C.I. decreases and the realized biomass of both species varies in the opposite direction. A larger difference in feeding rate would generate an increase in total productivity.

e) FEEDING RATE and CRITICAL SIZE POSITIVELY CORRELATED

CM = 0.48

CS = 0.50

RM = CM x 4

RS = CS x 4

CRITICAL SIZE M = 0.684

CRITICAL SIZE S = 0.750

As the frequency of simulans decreases, total PRD is almost constant but C.I. and both realized biomass increase.

f) SAME GROWTH RATE BUT DIFFERENT CRITICAL SIZES

CM = 0.48

CS = 0.50

RM = RS = 1.92

CRITICAL SIZE M = 0.750

CRITICAL SIZE S = 0.684

Decreasing frequency of simulans entails increasing productivity, decreasing C.I. and increasing realized biomass.

These results are shown in Table

TABLE 39 CI = RZM-RZS

	TOTAL PRD			REALIZED BIOMASS						C.I.		
Freq.	0.25	0.50	0.75	0.25		0.50		0.75		0.25	0.50	0.75
of m				m	s	m	s	m	s			
a	0.857	0.857	0.857	0.571	0.626	0.571	0.626	0.571	0.626	-0.055	-0.055	-0.055
b	0.767	0.815	0.844	0.421	0.978	0.360	0.837	0.309	0.719	-0.557	-0.477	-0.410
c	0.853	0.856	0.854	0.788	0.568	0.726	0.524	0.671	0.484	0.215	0.202	0.187
d	0.853	0.856	0.853	0.484	0.671	0.524	0.726	0.568	0.788	-0.187	-0.202	-0.219
e	0.853	0.855	0.854	0.568	0.719	0.524	0.663	0.483	0.612	-0.150	-0.139	-0.128
f	0.811	0.822	0.834	0.540	0.593	0.548	0.601	0.554	0.609	-0.052	-0.053	-0.054

From this analysis, we can see that not one of BARKER and PODGER's suggestions (a,b or c) really fit their data. On the other hand, our (d) and (f) cases both fit the data, the latter giving the closest approximation. This

does not mean that the growth parameters used in this simulation are necessarily the ones we would find in real situations: only that a physiological study of the two competing species could provide us with the elements needed to predict with exactitude the outcome of competition under various environmental conditions. This type of model-building is extremely relevant in showing that a detailed physiological study of growth is a necessary and sufficient condition for predicting the outcome of larval competition.

DISCUSSION

The problem of stabilising selection of the mean of a quantitative character and that of maintenance of genetic variance for that character are intrinsically related. In the past several models were proposed to explain these two phenomena; however little evidence was collected for the critical study of stabilising selection. What is more serious, little attempt was made to investigate beyond the functional relation of the character with fitness in a way that would allow us to make predictions as to the consequences of future change in the genetic structure of the population; also no attempt was made to locate the population in a proper ecological framework, when studying it.

Given the above restriction on earlier work on this topic we must now point out that there are two attitudes of mind that a student of these problems may adopt: the first one is finding the functional relationship of the character under study with fitness. This approach although an essential first step for future work on the problem is, when taken isolatedly as some investigators did (BARNES, 1969; KEARSEY and BARNES, 1970; LATTER, 1958) a dead end: no future knowledge is likely to come out of it since the last experimental design was not conceived with the aim of identifying the causes of the variations in fitness. The same criticism would apply entirely to most of the experimentation on the subject of competition (intra or interspecific) where the detection of a difference between populations or species should be envisaged not as a final mark but as the first step in the understanding of the

determination of competitive ability. The second approach, the one followed in our experiments, was to use the knowledge provided by studies on selection for body size and on competition between the selected and the unselected as the key to the understanding of the physiology competition through the use of suitable system analysis. Also, using this knowledge we were able to make predictions about the consequences on fitness of further physiological change consequent to selection for body size, and build a model of the genetic control of the character that would express itself physiologically in the manner observed. This model would also have to fit the results of orthodox genetic analysis done previously on our character, body size (FORBES ROBERTSON , studies in quant.inh.) and KEARSEY 1967.
and/KOJIMA). In other words we used a different approach from that used by previous workers on this and other subjects of population genetics: out of some physiological knowledge we produced a genetic model whose consequences on the character and on fitness had to be worked out after the model was built. The fitting of this model to the real data could then be only a matter of choosing the right constants.

We began by studying the problem of stabilising selection and by trying to define a way of measuring the changes in fitness which are consequent to selection. After considering several operational definitions

fitness we decided that competitive ability was the best because it represented the result of the growth process which involved the whole life history of the individual. In the sense that we are dealing with changes of fitness consequent to genetic manipulations like selection inbreeding and crossing, the study of those changes in the characters studied is necessarily a study of the changes in competitive ability. ALAN ROBERTSON (1967) pointed out that "discussions of the effect of natural selection on a metric character, based only on the phenotypic relationship of the character to reproductive fitness, are meaningless". There is little virtue in identifying the changes in fitness if we cannot make use of them to identify ultimately the genetic structure of the character and the way in which these changes in the genetic component can affect fitness. This attitude lead us to study the physiological basis of competition and then try to identify the particular type of gene action controlling the stability of the character.

In our studies of competition we managed to identify some of the physiological parameters responsible for differences in competitive ability. For example the difference in competitive ability between the Pac WT and the Pac W populations can be traced back to a difference in feeding rate. In the same way we managed to detect an increase in the feeding rate of lines selected for large size

and a decrease in the lines selected in the opposite direction. We also found it necessary to postulate an increase in the critical weight of the large line to account for its non-improvement in competitive ability.

However, this is not the end of the story. Several questions came to our mind: Why does the decrease in feeding rate of the low line produce a reduction in adult body size, and a similar decrease in the Pac white population does not? Or, what is the nature of the correlation between feeding rate and critical size observed in the high line? How does inbreeding affect the growth ability of the individuals such that both selected lines and the unselected exhibit a decrease in competitive ability and in body size? Is there any reason which could prevent relaxation of selection from bringing the mean of the selected lines back to the unselected level? All these questions can only be answered when we know the genetic mechanisms controlling growth and analyse the results of our genetic manipulations and do some model building aiming at fitting these results to the predictions made with the aid of the model.

When discussing the physiological basis of competition we considered several indicators of competitive ability, namely, differences in development time, differences in body size within days and differences in productivity. We assumed that if there was no difference in the growth processes underlying competitive ability, individuals with the same development time should have the same body size. This is true for competition under any circumstances (variable proportion or time course) between our Pacific WT and W populations. Failure to verify this in competition experiments between unselected line and lines selected for body size implies that the same development has been achieved through different physiological processes which affect either feeding rate and/or the efficiency of food conversion, and/or critical size. If the duration of the post-critical growth period is fixed (FORBES ROBERTSON, EC.Gen.; BAKKER, 1961) and if the genes affecting growth in the two periods are the same, two situations can be responsible for the response to selection for body size: either there is large variation in the critical size or, in the absence of this variation, changes in feeding rate, and efficiency would have to be negatively correlated in the low line; in the large line there would have to be a positive correlation between feeding rate and efficiency but this would improve the competitive ability of the flies in relation to the unselected, which is not observed. The variation in critical size would have to be

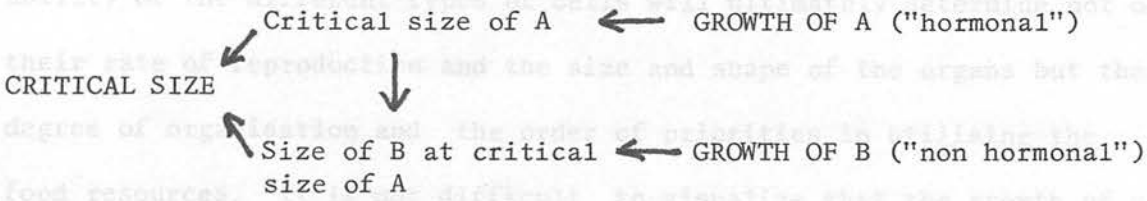
quite substantial to account for the differences in body size at the end of the larval period. This is not likely to occur since natural selection must have minimized critical size in the course of evolution. On the other hand if critical size showed such a large amount of genetic variation, we would have to postulate a very complex gene-environment interaction to explain why the development time of the small line is not reduced under optimal conditions, and why the large and the small lines show a similar development time when in competition with each other. The second alternative (negative correlation between feeding rate and efficiency in the small line) is easily eliminated when we recall that our experiments indicated clearly that small flies eat less than unselected or large flies, and that large flies eat more than the unselected. We are then faced with an apparent dilemma; if the differences in critical size are not large enought to account for the differences in adult body size, how can we have flies with very dissimilar body size but similar development time? Two alternatives face us: either we have a large degree of independence in the genetic control of the two growth periods or we have phenotypic variation of critical size, this variation being more marked in the selected flies than in the unselected. The first hypothesis is immediately ruled out on the grounds that independance of the two growth periods which could account for the differences in body size and which would be operative through a decrease and increase of growth rates during

the post-critical period (in the small and large line respectively) would leave the competitive ability of the two lines unaffected and this is not observed. When considering the second possibility we had in mind some experiments done by FORBES ROBERTSON (EC.Gen.No.6) in which data presented can only be explained if we assume a phenotypic variation of critical size. In short, the estimate of critical size from growth under unrestricted conditions when extrapolated to individuals grown under restricted conditions (live yeast crowded or low protein axemic) allows us to make a prediction about the development time of the flies which differs from the actual observed value. This implies phenotypic variation in the critical size. FORBES ROBERTSON (op. cit.) also found that lines selected for large body size under low RNA conditions showed a reduced capacity to pupate compared to unselected when the latter reached critical size (50% pupation). Thus it was proved that critical size can be increased both genetically and phenotypically. If we bear in mind that the critical stage is probably the result of hormonal and other interactions between different organs and that body sixe is the sum of growth in several different components it is easy to conceive that some organs will be more important than others in determining the developmental changes we refer to as the critical stage. These organs will have to reach a certain minimum size to be effective in producing the substances through which development is controlled (see HARRIS, 1970). If we accept this, it is clear that some genetic variation in critical size will

exist, due to variation in those components of the body not directly involved in the production of the controlling substances - "hormones". We would then have two types of organs, the ones producing "hormones" and the ones affected by them. Each of these organs has a regulating influence on the other, but of a different type: the "hormonal" organs produce substances that stop or change the course of development, (e.g. ecdysone and its action in pupation) very much in the way a fixative acts in the course of the preparation of a slide for microscopic examination; the "non-hormonal" organs act on the "hormonal" organs in the way that a minimum size of these organs is needed for development to proceed. This mutual regulation of the two types of organs provides us with a link with the evolution of this regulating system: whenever the growth of the two types of organs is synchronised the best combination of organs will be acheived. An organism with a fast growing "hormonal" organ will reach a corresponding autogenetic stage earlier and therefore would be fitter, but if the growth of the "non-hormonal" organs is not as fast, then at the critical stage there will not be enough biomass for the "hormones" to act upon and the fitness of the individuals concerned will be seriously affected: SANG (1949) and BAKKER (1961) found evidence that the viability of the pupae of Drosophila increases with their size. On the other hand a slow growing "hormonal" organ will be less fit due to the increase in the development time of the individual as well as uneconomical since it would require more food to reach the critical stage.

We summarized these conclusions in the following diagram:

DIAGRAM 3



It is clear that natural selection will have acted in favour of those individuals which show the fastest growth under certain ecological (nutritional) conditions. These individuals would be the ones that show a "balanced" growth, i.e. the two components of the body increase their size in a synchronized way so that A reaches its critical stage in the shortest possible time when B is at the minimum compatible with maximum viability As we saw before there are two ways of unbalancing this system. The first one coincides with a faster growth rate for A than for B and vice versa for the second. The consequences on fitness are different: In the first case the components of fitness that will be mainly affected are viability and potential egg production; in the second case development time would be the main component of fitness to be affected, but body size would be increased.

Up to now we have dealt with the growth of the two components as independent events. In reality this does not happen as all the organs of an organism are very much interdependant to the extent that they depend for gorwth on a common food pool. Indeed each of the cells

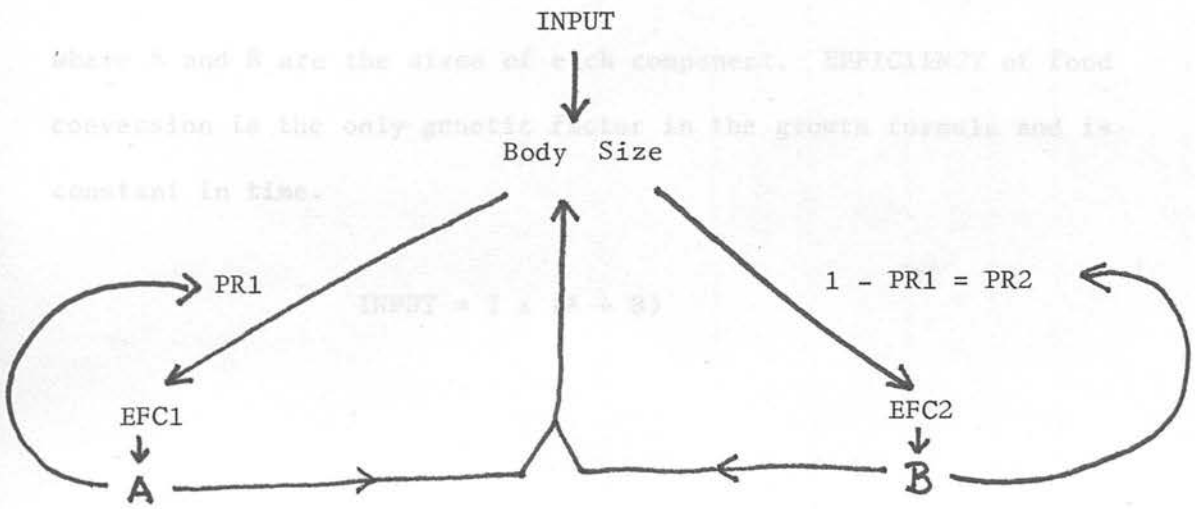
or organs of an organism has to compete for food to a variable degree with the rest of the cells or organs in the same organism. The competitive ability of the different types of cells will ultimately determine not only their rate of reproduction and the size and shape of the organs but their degree of organisation and the order of priorities in utilising the food resources. It is not difficult to visualize that the growth of cells in an organism is different from growth in a Petri dish where the nutrients are readily available to the thin layer of growing tissue. In an organism the nutrients will be distributed according to a system of priorities, some organs getting more than others. This system will be operative at all stages of development. Examples of this would be two cells with different nuclear-cytoplasmic ratios the one with a larger cytoplasmic offering a larger surface of absorption, therefore having higher priority than the other; at a more advanced stage this system of priorities could be represented by the differences in blood irrigation of different organs, some organs getting more blood than others. Therefore all the food that gets into a growing system will be distributed according to a system of priorities. We can reasonably assume that these priorities at a certain time will be positively correlated with the size of the organs at that time.

Once the food reaches the organ it is transferred into living material at different rates, according to the efficiency of the cells concerned. Different genetic or epigenetic combinations are likely to exhibit different rates of cell reproduction, and represent the genetic component of growth.

The nutrients that reach the cell were probably assimilated in different ways but their amount must be a direct function of body size.

Having considered the factors likely to affect the relative growth of components A and B we shall now summarise them in the following diagram:

DIAGRAM 4



We are now in a position to simulate in a computer the results of assigning different values to EFC1 and EFC2, the only genetic variables present in this system.

The increase in body size per unit of time will be the sum of the partial increases in components A and B. The increase in each of these components at time t is equal to

$$\Delta X = X_o + \text{INPUT} \times \text{PRIORITY} \times \text{EFFICIENCY OF CONVERSION}$$

Where X_o is the size of the component at time t - 1, INPUT is the food input which is a direct function of body size, Priority A is calculated from the following formula:

$$\text{PRIORITY A} = 0.5((A-B)/A + B)K$$

$$\text{PRIORITY B} = 1 - \text{PRIORITY OF A}$$

where A and B are the sizes of each component. EFFICIENCY of food conversion is the only genetic factor in the growth formula and is constant in time.

$$\text{INPUT} = I \times (A + B)$$

TABLE NO. 39

SIMULATION OF GROWTH (COMPETITION BETWEEN COMPONENTS OF BODY SIZE)

I			1		2		3		4		5	
EFC1	EFC2	D	T	SIZE	T	SIZE	T	SIZE	T	SIZE	T	SIZE
1.025	1.01	+0.015	58.10	17.89	29.96	18.25	20.48	18.39	15.74	18.52	12.90	18.66
1.025	1.025	0.000	60.00	20.00	30.69	20.00	20.95	20.00	16.06	20.00	13.12	20.00
1.025	1.040	-0.015	62.37	23.13	31.84	22.26	21.53	22.28	16.44	22.00	13.39	21.79

I = LEVEL OF FEEDING

EFC 1 and EFC 2 are the efficiencies of food conversion of "hormonal" and the "non-hormonal" components respectively.

D is the difference EFC1 - EFC2

The examination of Table No. 39 reveals that in individuals possessing a positive D (the hormonal organs grow faster than the non hormonal) the development time is always shorter (within levels of feeding) than the development time of the balanced individuals (D = O). However, this apparent advantage is opposed by the reduced viability of these individuals since their non-hormonal biomass is not sufficient to allow development to be completed successfully. This reduction in viability is negatively correlated with the level of feeding, since adult body size will also be reduced, it is natural to expect a reduction in egg production.

The individuals possessing a negative D will always exhibit an extended development time compared with that of the balanced individuals. This effect will persist independently of the level of feeding .

The differences in body size between the unbalanced and the balanced individuals tend to be buffered as the level of feeding increases. This is a remarkable property of this system since it will mean that the fitness of the individuals is very much a function of the level of feeding that they experience, i.e. an individual with a positive D is more viable, under optimal conditions than under competitive conditions. The reduction in viability in individuals with reduced body size resembles singularly the reduction in viability observed commonly in lines selected for small body size. On the other side, individuals with a negative D will never show a reduction in viability since the biomass of the non-hormonal organ is always greater than it

needed be. However, if the unbalance is so great that the critical stage is never reached then viability will be affected. This could be the situation in the giant gene system; also our own experience tells us that in the culture under optimal of lines selected for large size non-pupated larvae can be observed regularly when all the other insects have reached the adult stage. If we consider the relative changes of the two parameters studied, body size and development time under variable conditions of feeding we can see that they are affected differentially. Increasing the feeding level 5-fold reduces the advantage in development time of the +D individuals from 0.031 to 0.016 ($\frac{0.031}{0.016} = 1.937$); the disadvantage in size is reduced from 0.105 to 0.067 ($\frac{0.105}{0.067} = 1.567$). The same phenomenon in reverse happens with the -D individuals. Also, within feeding levels the percentage difference in body size is always greater than the percentage difference in development time. The conclusion that we draw from this analysis is that development time is a "character" better buffered than body size, therefore shows less variation.

Another point to be noted concerns the fact that at high feeding levels (I = 5) the differences in development time may be too small to be picked up by natural selections, thus creating a plateau of individuals with different body size but similar fitness. Or else, the disadvantage of the +D line in body size (and consequently in viability and potential egg production) may be compensated by its advantage in development time. In the same way the disadvantage of the -D individuals in terms of development time may be compensated by its potentially increased capacity

of egg production. The results of the experiments on egg production show that the increase in body size of the large line is wasteful as far as egg production is concerned. There is no doubt, however, that whether this compensation exists or not the D= 0 individuals represent the best compromise between a fast development and a high viability; this compromise will be at the root of the stabilization of body size at the critical stage (and/its correlate, adult body size) at the value of 20.00.

At a given time the amount of food ingested by growing individual is a direct function of its body size at that time. It is not difficult to see that this amount will be positively correlated with D. The amount of food ingested by unit of time at a fixed time is nothing but what we have been calling the feeding rate or appetite. In this way we can see that there is no need to postulate the existence of genes controlling the input of food through changing the behaviour of the larvae, although these changes might be present. We can also see how feeding rate or input will be affected by the intensity of food restriction, being another effect of the interaction between genotype and environment. An example of a change in feeding rate which was not caused by an unbalance in growth and is probably behavioural in origin is the one observed in the Pac W population when compared with the Pac WT. In this case the white gene reduced the mean feeding rate of the population leaving its variance untouched. Thus we have a system which, by controlling the growth in two components of the body which compete for food resources with each

other, gene rates variation in the body size at the critical stage. This variation is genetic in origin since it depends on the particular values assigned to the efficiency of food conversion, but it is also subject to environmental variation (food supply) due to the competitive nature of growth in the 2 components.

We now return to our original dilemma, that of finding a way in which differences in adult body size can be explained without having to postulate a large genetic variation in critical size nor any complicated hypothesis involving different growth rates for the two growth periods. If the genes controlling critical size, in other words the genes controlling the efficiency of food conversion in the "hormonal" component showed a large amoung of additive genetic variation one could perhaps try to explain the differences in body size as being caused by this variation. But we would immediately face unsurmountable difficulties in the small line the competitive ability would increase substantially as the deviation from the mean increased, therefore fixation would occur for the gene which reduced critical size most. Development time measured under optimal conditions would also be reduced.

The large line would show a sharp decline in competitive ability but the early productivity of the cultures would not be affected.

None of these predictions conforms with the results obtained by us. Therefore we shall conclude that the changes in growth responsible for changes in body size on selection are not likely to be of an

"instantaneous" nature, like " pure" changes in critical size. Instead, we propose that the changes in critical size suggested by various evidence are the result of more profound changes, which act for longer periods on the growth ability of the individuals. These changes, intially of a minor nature may be amplified substantially if the growth of several components of the body is interrelated and of a competitive nature. Alternatively, the results of simulation of "instantaneous" changes like changes in the initial proportions of the two components which nevertheless have the same efficiency (D = O) shows that even large deviations from equality tend to be buffered as growth progresses.

Let us now turn to the implications of the model of growth on a genetic scale and try to see what the consequences are on competitive ability and body size. All the researchers who have studied the genetic architecture of body size agree that this character is governed mainly by additive gene effects and additive x additive interactions. Therefore we feel justified in eliminating other types of genetic variation from our model-building. In our table No.40 the efficiency of food conversion of the "hormonal" component was kept constant and only the efficiency of the "non-hormonal" component varied; we saw that when the value for the efficiency of this component was intermediate, the fitness of the individual was highest (D= O). We can turn this into a genetic model where two loci α and β control the hormonal and non-hormonal components of the body, respectively and in the manner described. The α locus would be in a homozygous state and only the β locus showed variation. If this variation is additive the intermediate value will correspond to the heterozygote. Therefore variation will be

maintained at this locus.

If we now consider the effects of introducing variation in the α locus we will have 9 genotypic combinations whose frequencies will depend on the frequencies of the allele, at each locus as well as on the intensity and type of linkage (if any) between the two loci.

In order to make possible the simulation of growth we shall assign numerical values to each of the alleles at the α and β locus, although this may deprive the solutions found from the generality they would have if an algebraic approach had been used.

When the values assigned were similar for each locus, in other words when A = B and a = b the double homozygotes $\frac{AB}{AB}$ and $\frac{ab}{ab}$ would be as balanced as the double heterozygote $\frac{AB}{ab}$. However $\frac{AB}{AB}$ would have a faster rate of growth therefore would be fitter than the double heterozygote and fixation would ensue for genes A and B. Since this is incompatible with the amount of additive genetic variation normally present in populations of Drosophila we rejected these values.

However, when we assign different values for the alleles at two loci in such a way that their mean value is the same we find that all but the double heterozygotes are unbalanced to a variable degree and in different ways. The values assigned under these conditions were:

A = 1.03, a = 1.02

B = 1.04, b = 1.01

TABLE NO. 40

SIMULATION OF GROWTH FOR THE TWO-LOCI MODEL

				I = 1			I = 5					
Genotype	D	EFC 1	EFC 2	T	INPUT	BODY SIZE	T	INPUT	BODY SIZE	RF = 0. 5	RF = 0.2 COUPLING	RF = 0.2 REPULSION
Ab/Ab	+0.02	1.03	1.01	57.00 57.55	16.24 16.70	17.55	12.00 12.76	60.87 72.68	18.24	0.0625	0.01	0.16
Ab/ab	+0.015	1.025	1.01	57.00 58.10	16.11 17.03		12.00 12.90	60.51 74.38	18.66	0.125	0.08	0.08
ab/ab	+0.01	1.02	1.01	57.00 59.03	16.00 17.69	18.59	12.00 13.03	60.17 76.06	19.06	0.0625	0.16	0.01
AB/Ab	+0.005	1.03	1.025	57.00 59.06	16.53 18.34	19.28	12.00	61.83	19.53	0.125	0.08	0.08
AB/AB	0.00	1.025	1.025	57.00 60.00	16.42 19.08	20.00	12.00 13.12	61.49 77.48	20.00	0.250	0.34	0.34
aB/ab	-0.005	1.02	1.025	57.00 61.00	16.31 19.92	20.94	12.00 13.26	61.15 77.30	20.56	0.125	0.08	0.08
AB/AB	-0.01	1.03	1.04	57.00 61.15	16.87 20.81	21.80	12.00 13.23	62.86 83.48	21.10	0.0625	0.16	0.01
AB/aB	-0.015	1.025	1.04	57.00 62.37	16.77 21.99	23.13	12.00 13.39	62.53 86.61	21.79	0.125	0.08	0.08
aB/aB	-0.020	1.020	1.04	57.00 64.00	16.68 23.73	24.95	12.00 13.57	62.21 89.76	22.57	0.0625	0.01	0.16

I = level of feeding; EFC 1 and EFC 2 are the efficiencies of food conversion of the "hormonal" and the "non-hormonal" components of growth; T = time at which the hormonal component reaches its critical size = 10.0; D = EFC 1 - EFC 2; RF = Recombination fraction.

In this way the variation in gene values at the α locus is smaller than at the β locus. This introduces a positive correlation between the sum of the gene values and D (=α-β). Since the two loci act additively on body size we expect the sume of gene values to be an indicator of growth rate, therefore negative values of D should be associated with faster growing individuals and positive values of D with slow-growing ones. This correlation fits well the conclusions drawn from our experiments that the small line (+D) is a slow grower and the large line (-D) a fast grower if we consider growth rate as the increase in body size per unit of time.

To avoid an artificial situation we used very small deviations in gene values oscillating between 1 and 3% approximately with an average of 1.5%.

The results of the simulation at two feeding levels are shown on Table 40.

We can see that both D and development time are positively correlated with body size under these circumstances. This would mean that the small flies could develop faster than any of the others and would therefore be fitter than the unselected. This apparent contradiction is easily eliminated when we look at the values for food input at a fixed time. These values represent the ability of the flies to utilise the foot existent in their environment. In a competitive live-yeast system this rate of cropping the yeast

The third and last way in which the balanced individuals might be "protected" from competition by the $\frac{AB}{Ab}$ individuals is by linkage. GALE (1968) and KEARSEY looked at the possibility of establishment of equilibrium for a character controlled additively by two loci in which fitness is proportional to the mean phenotypic value of the genotypes and falls on either side of the optimum represented by the double heterozygote. They found that provided the two loci do not differ very much in their action on the character stable equilibria will occur only if the two loci are linked, the intensity of linkage required falling off as the disparity between loci increases. The examination of Table 40 shows that the frequency of the above referred genotype is reduced by linkage, but the type of linkage (coupling or repulsion) has no effect on it. Complete linkage will obviously eliminate this genotype from the picture. However, we feel that this last approach has a touch of pragmatism in it and consequently we favour the 2nd hypothesus since it is supported by the fact noted in many of our experiments of selection for body size, where deviations in body size did not reduce significantly the competitive ability.

Further evidence for this point comes from our experiment in selection for development time. If the fast developing flies in pure culture have reduced competitive ability when in competition with the intermediate flies, how can we explain the fact that selection for fast development time did not reduce competitive ability? The answer may lie in the fact that selection for fast development time will tend to increase the proportion of $\frac{AB}{Ab}$ individuals in the culture.

population will mean that under pure culture conditions the small flies will develop faster than any of the others not only because they have a low input per capita, but also because they reach the critical stage at an inferior size. In mixed culture the low input of these flies, caused by a smaller body size will generate a decrease in competitive ability when compared with the competitive ability of the intermediate (balanced) flies. The higher input of the large flies is not enough to counteract their unbalanced growth, even when the sume of the values for efficiency is at its highest, (1.03 + 1.04) at least for the values of efficiency considered here.

The only anomalous case is the one where the efficiency of $\alpha = 1.03$ and that of $\beta = 1.025$. In this case, although body size at the intial stage (and adult body size) are smaller than the same values for the balanced individuals, both development time and food-input are higher than in the balanced, suggesting that fixation for the A gene at the α locus might occur. The only factor capable of reducing this advantage of the partial homozygote $\frac{AB}{Ab}$ over the double heterozygote $\frac{AB}{ab}$ is the reduced viability of the former. The second way in which this advantage might be reduced is by reducing the variation at the α locus to such an extent that the differences in fitness between the two partial homozygotes $\frac{AB}{Ab}$ are so small that natural selection will be unable to pick them up. This is even more true when we think that development time of Drosophila IS SUBJECT to circadian variation and that minor differences in development time will be not discriminated from.

Selection for slow development time would include both large and small individuals therefore dissortative mating between these partial or total homozygotes for different alleles will increase enormously the number of heterozygotes in the population, thus reducing the segregational load. The fact that the body size of the slow line is increased compared with theunselected must mean that the development time of the small individuals (+D) deviates from the unselected less than the large individuals (-D) do. The fact that cultures of unselected populations of Drosophila, under competitive conditions (initial variance in the age of the egg no.) show a pattern of body size which decreases from the first day of hatching to the second and then increases progressively until hatching is completed, supports this conclusion. It could be argued that these differences in body size are onlythe result of different amounts of food available to the larval during the post-critical period. If this was true then selection for body size under competitive conditions should be ineffective. Our selection experiment No. 3 performed under competitive conditions with a large initial variance in the age of the eggs gave values for the response that are incompatible with the argument that size differences between days in a culture are only of a phenotypic nature.

Let us now consider in more detail the two-locus model and the consequences of selection away from the mean on the response, competitive ability of the selected flies and the productivity of the cultures and ultimately on the gene frequencies at the loci are concerned.

An analysis of the Table No.41 shows that D is positively correlated with body size. The table also shows that the variation in D observed in individuals close to the mean value is generated by variation at the α locus (homozygosity for each of the alleles at this locus) with constant heterozygosity at the β locus. Greater deviations exploit variation at the α locus, the β locus having reached fixation for different alleles on each side of the mean. If we assume that selection for large and small size will increase the frequency of the genotypes showing higher absolute values of D it is clear to see that fixation will be rapidly achieved, in this two-loci system. If this is true, selection away from the mean will tend to create irreversible situations which would prevent relaxation of selection from bringing the mean value of the metric character back to the unselected value. One could argue that since back selection is effective in bringing the character back to the unselected value, this argument would still hold. This point can only be fully explained by doing extensive studies of the competitive ability of back selected lines with the aim of studying their physiological behaviour in terms of growth. Our own experiment was not particularly illustrative in this respect, and we did not find appreciable differences in competitive ability between selected and unselected individuals. Also, the experiments on back selection for fast development time in lines selected for body size wre not very conclusive, due to the poor performance of the control.

If lines in which selection was relaxed for a large period of time under apparently appropriate ecological condition (cages) and little or no return to the mean is observed we must conclude for one of two possibilities.

a) There was fixation for at least one gene which will not allow the population to come back by itself to the original value. The best the population can aim at is an increase of the frequency the less unbalanced genotype possible with the array of genes present. However, in our two-locus system, ifffixation occurs at the β locus then selection for competitive ability (always present in any culture) will favour the extremely unbalanced (+0.02) individuals since they have the highest input leading to complete fixation ($\frac{Ab}{Ab}$). In the large line the outcome of competition within the line will be the selection of the less unbalanced individual which also happens to be a double homozygote ($\frac{AB}{AB}$), since it has the highest competitive ability and the shortest development time.

Therefore, fixation at one locus only will automatically lead to fixation at the other locus, under the conditions postulated by this system.

However, fixation at both loci will mean different degrees of unbalance for both lines (+0.02 and =-0.01 for the small and the large lines respectively) since homozygosity in itself is not important, only the degree of unbalance caused by it.

This situation is likely to be observed in lines selected for long periods as many of the bristle experiments are (ALAN ROBERTSON, 1967). In this case even when the lines respond to back selection for the character we must bear in mind the possibility that other sources of variation may have been exploited and that only a careful competition study will reveal differences in fitness and physiology between lines with apparently the same body size.

This could be one of the factors responsible for the differences in opinion between ALAN ROBERTSON and the Birmingham School about the importance of the association between sternopleural bristle number and fitness. ALAN ROBERTSON claims based on the results of relaxation of selection in his highly selected lines and the fact that there is little or no reversion to the mean, that bristles are a trivial character. On the other hand KEARSEY and BARNES (1970) using a population derived from crosses between selected inbred lines claim that the reduction in the variance of bristle number observed when flies are moved from optimal conditions to competitive ones is good evidence that the tails of the distribution of bristle number are more affected than the mean. We can immediately see the difference between the two approaches and the different consequences that will follow.

One important point we must make here is that relaxation is always conducted under pure culture conditions, therefore the selected flies are never allowed to compete with unselected. In nature some migration will occur eventually and this has the two-fold effect

of eliminating the weaker population if they do not interbreed (case of competition between sibling species) or if the selected population is "stuck" at a given phendype value for lack of appropriate genetic variability these immigrants would provide her with the necessary genes which could bring the mean value of the population back to the unselected value.

It would be extremely interesting to study the effect of "injecting" new genetic material (probably provenient from inbred lines derived from other selected populations) in populations that have been relaxed for long periods without showing any reversion to the mean.

b) Once we have discussed the genetic component of body size it is now time to turn to details in the ecological systems used. We have seen, in connection with our discussion of the results published by AYALA (1971) how ecologically irrelevant was the "serial-transfer-system" used by this author, since it gave no importance at all to development as a component of fitness. In this sense our population cages in Edinburgh with their weekly or two-weekly intervals of introduction of new niches (pots) tend also to underestimate the importance of development time. The Birmingham school uses population cages of the TEISSIER type where a new niche is introduced daily or every couple of days, thus being ecologically

more relevant. Obviously one would get different selection pressures acting in each system and that could account partially for the difference in the results obtained.

Another feature of the results of simulation of selection for large and small body size is that if we exclude the mildly unbalanced partial homozygotes (D = $\pm$ 0.5), the competitive ability of the large individuals will decrease progressively as the examination of the values for input at a fixed time (= 57.00) will reveal. However, the same will not be observed in the small line where selection will go through a minimum at D = +0.01 (INPUT = 16.00) and then increase slowly up to D = +0.02 (INPUT = 16.24). Under these circumstances we would get a continuously decreasing curve for selection for large body size but one with a minimum rising slowly but never reaching the unselected value. This will lead to difficulties in fitting a regression line to the decrease in competitive ability with selection for small size. The regression coefficient will be reduced, compared with that for the high line and its variance will be greater.

INBREEDING The consequences of inbreeding from selected lines and unselected will depend very much on -

a) The deviation of the selected lines from the unselected, since the frequency of the genes involved will vary.

b) In the unselected inbreeding will be a random process and considerable variation between inbred lines should exist. This variation should be more limited in the selected lines.

c) The linkage relationships between loci and genes.

We have seen from the analysis of our model that the same level of homozygosity either partial or total corresponds to different values of fitness and body size. Under these conditions, inbreeding from the selected lines will lead to fixation of the particular allele which happens to be more frequent as a result of selection. As selection necessarily increases the frequency of one allele at the expense of its alternative allele (9) the results of inbreeding should be different for the selected and unselected. The inbred lines originated from unselected will include the inbred lines from both the large and small lines, provided a sufficiently large number of lines is studied and that recombination has not altered the linkage relationships during the course of selection. Our first generation of inbreeding supports the conclusion that the selected and unselected flies are differentially affected.

Our analysis was not designed to study differences between inbred lines within selected and unselected lines. It would be interesting to examine the results of inbreeding in selected lines which deviate to a different extent from the unselected level, since this would help us to "isolate" the genes involved and study the results of crossing between them.

Crossing inbred lines within selected and unselected may not help the lines much if there was not much variation left at the beginning of inbreeding.

A final point concerns the evolution of the genes controlling quantitative genetic variation.

We have seen that homozygosity in itself is not a disadvantage since we have two types of double homozygotes with quite different values of D and therefore of fitness. We can also envisage easily a situation where the α locus is homozygous for gene $\bar{A}$ with a value of $\frac{A + a}{2}$ and the same for the β locus - $\bar{B} = \frac{B + b}{2}$, therefore A = B. In this situation the homozygotes partial or total ($\frac{AB}{Ab}$, $\frac{AB}{ab}$, $\frac{AB}{AB}$) would be as the double heterozygote $\frac{AB}{ab}$. This however is inconsistent with the large amount of additive genetic variation for body size detectable in populations of Drosophila. Since one cannot rule out the possibility of the coexistence of genes like A and B in the course of evolution one is left with two alternative explanations:

a) That heterozygosity is "good" in itself and therefore a balanced heterozygote ($\frac{AB}{ab}$) would be superior to a balanced homozygote ($\frac{AB}{AB}$). Although many people have speculated on the possible reasons for this heterozygote superiority (LERNER, 1954) there is still some mystery attached to it.

b) A more plausibe explanation is one which involves the reaction of an already established balanced system to the introduction of a new gene. If the new gene has the same phenotypic value as the gene it substituted, there will be no change at all in the balance of growth, therefore in fitness. A new gene with a different value from the one it substituted will be immediately selected against, since it

would unbalance growth. Even when its phenotype value is equal to A or B they will never get to the homozygote stage. Exceptions to this rule will be observed when there is a double change at the same locus, such that the two alleles have suffered compensatory change and the average effect of the locus remains unchanged or when a change at one of the alleles at locus α is accompanied by a change in one of the alleles in locus β so that no unbalance is reached. In any case a simultaneous change in two loci is necessary and a very particular one as we were able to see which gives the event a very low probability of occurrence. In this way balanced systems are very resistant to change brought about by such agencies at mutation.

In this light we must consider the results of our experiments on the coadaptation of genes in the Pacific and Kaduna populations. As we saw the results of these experiments suggest clearly that the two populations do not differ in the genes controlling growth, therefore body size. We have no estimate of the difference in evolutionary terms between the two populations, but it is likely that many generations have been spent in geographical isolation and during this time no change in the growth detectable by our methods has occurred. As we saw from the results of this experiment the two wild-type populations, although differing slightly in body size measured under optimal and competitive conditions show comparable values for competitive ability.

This fact suggests that the genes involved in the control of growth, therefore in the control of competitive ability, are not different in both populations. The difference in body size would then be a consequence of change in some growth parameter not correlated with competitive ability. In the same way the dramatic inferiority in body size of the white Kaduna population, measured under competitive conditions, associated with a marked reduction in competitive ability indicates that the genetic component of growth responsible for the competitive ability was affected. The fact that this population does not differ in body size measured under optimal conditions from the WT Kaduna suggests again that there are growth parameters which are not correlated with competitive ability.

To conclude this discussion we will say that although the evidence for stabilising selection for body size is not as conclusive as one would have liked it to be, there is no doubt that large changes in the growth pattern of the individuals were created by selection for body size. Given a restriction in the feeding opportunities these changes must have some consequences on the cultures involving these individuals, consequently on their productivity pattern of the competition affected by them. Given a suitable system and means of analysing it the knowledge of the physiological parameters of strains of Drosophila enables us to predict in a deterministic way the outcome of competition between these strains.

What we are not able to do at the present time is to determine the way in which the variance of the growth parameters (therefore body size) is affected when selection for body size is carried out. Changes in this variance are likely to affect the outcome of competition, between strains which differ markedly in body size, in such a way as to reduce to zero the differences in competitive ability. This means that only the use of a genetic model, which would enable us to calculate the changes in frequency of the different genotypes with selection will allow us to estimate the changes in the variance of the growth parameters controlling body size and competitive ability.

We could then construct a model for competition which would take into account these changes in variance and would allow us to estimate how much we should change the mean of the population before the effects of this change on fitness were greater than the compensatory effects of the changes in variance.

SUMMARY

1. The work presented in this thesis is concerned with the study of stabilising selection for body size in D.melanogaster.

2. The method followed in this study was to create differences in body size through selection and observe the changes in fitness associated with these differences. Also, once the differences were created, we observed the effects of natural selection on the selected lines when selection was relaxed.

3. The consideration of this problem involves the choice of a suitable estimate of fitness as well as the definition of a suitable ecological system in which fitness should be measured. We decided that the best indicator of fitness available is the biomass produced per unit of time in competition with a standard competitor, in a live-yeast system.

4. The physiological changes responsible for the changes in body size may or may not affect fitness, under the conditions described. Given hypothetical differences in physiological parameters like feeding rate, efficiency of food conversion and critical size we were able to simulate in a computer the outcome of competition between strains differing in one or more of these parameters. This allowed us to make predictions of the changes in competitive ability and the productivity of the cultures. Therefore we were able to analyse our results in terms of a system rather than in terms of individual characters.

5. It was found that the physiological changes responsible for the changes in body size of the selected lines were probably changes in feeding rate associated with changes in the critical size. However, the "nature" of growth is affected in this case since we can detect differences in body size in flies exhibiting the same development time. This change in the "nature" of growth can be explained if we postulate an unbalance of growth in the selected lines.

6. Although the changes in body size obtained by selection are quite substantial, it was difficult to detect a consistent change in compeitive ability measured against a standard competitor. It is suggested that this difficulty might be due to changes in the variance of the growth parameters correlated with changes in their mean. Within the range of deviations of body size from the unselected value these changes in variance would counteract the possible changes in fitness which are a consequence of selection.

7. Relaxation of selection for lines selected for large and small body size had little effect in bringing the mean value of the character back to the unselected level. One possible exception was verified when selection was relaxed in a population cage.

Back selection had an immediate response, similar to that of forward selection. The experiments which tested the competitive ability of the back selected lines were not conclusive. Selection for short development time in the selected lines did not affect body size; the changes in competitive ability were not well defined.

Selection for fast and slow development had some response when development time was measured under pure culture conditions. Under competitive conditions the apparent advantage of the fast line disappeared but the disadvantage of the slow line persisted. The response to selection for fast and slow development was accompanied by a reduction in body size below the unselected level in the fast line and an increase in the slow line above the same level.

8. Selection for large and small body size under competitive conditions showed some response in both directions though less well marked than when selection was carried out under optimal conditions.

9. Inbreeding caused a proportionally equal decrease in body size in all the lines. This decrease was more accentuated when body size was measured under competitive conditions. Competitive ability was affected differentially in the 1st generation of inbreeding, but this difference disappeared subsequently. Viability was reduced below the non-inbred level.

10. The experiments on egg production of the selected and unselected flies grown under different conditions in the larval stage fed different amounts of food in the adult stage revealed a superiority of the unselected over the selected lines.

11. The crosses between the Pacific and the Kaduna populations showed no breakdown or improvement in competitive ability in the F1 or the F2, suggesting that the genes controlling the growth ability which is correlated with competitive ability are the same in the two populations.

12. An attempt was made to establish the physiological basis of competition between populations of D.willistoni and D.pseudoobscura (AYALA, 1971) and D.melanogaster and D.simulans (BARKER and PODGER, 1970). This attempt consisted in simulating in a computer competition between species which differed in one or more physiological parameters, suggested by the data presented by the above authors, and observing the analogy between their results and the computer simulation results.

13. A model to explain the growth of lines selected for large and small body size as well as the unselected is proposed. This model has a genetic component consisting of differences in the reproductive rate of the cells of an organism (or efficiency of conversion of nutrients into biomass) and an environmental one which is based on the competitive nature of growth - the greater the efficiency the higher the priority in utilising the food input of an organism. In this model growth would be regulated by the interactions of two types of organs, "hormonal" and "non-hormonal". Variation in the "hormonal" organ would affect mainly the development time of the individual, whereas variation in the "non-hormonal" organ would affect their viability and body size.

14. On the basis of this physiological model a two-loci genetic model is proposed which would explain some of the changes in fitness on selection for body size, inbreeding and crosses between geographic populations.

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