The ecological genetics of growth in *Drosophila*

2. SELECTION FOR LARGE BODY SIZE ON DIFFERENT DIETS

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1. INTRODUCTION

When larvae from a wild population of *Drosophila* are grown on diets deficient in one or more essential nutrients, the within-culture variance of the body size of the adult flies is greater than on optimal diets. This increase has been attributed, in part at least, to the segregation of genetic differences which make little or no contribution under more favourable conditions (see the preceding paper). Hence the physiological changes which underlie the selection response for the same 'character', body size, are likely to vary according to the nature of the environment, although mere record of body size in a single set of conditions can throw no light on this possibility, which is relevant to the rate and extent of the response to selection and also the properties of the genetic variation of body size generally. The present paper describes the results of selecting for larger body size in environments which differ in the quality of the diet supplied to the larvae.

2. MATERIALS AND METHODS

A cage population of *Drosophila melanogaster*, known as *Pacific*, has been used in these tests. The preceding, introductory paper (Robertson, 1960) described the culture of larvae on aseptic, synthetic media and also the reasons for choosing a log scale for both body size and the duration of larval life. Body size is expressed as three times the natural logarithm of thorax length, measured in $\frac{1}{100}$ mm. A unit difference on this scale corresponds to a unit difference in log weight.

The synthetic media used in two of the selection experiments were: (i) a protein-deficient medium with 2% casein in place of 5% in the 'complete' Medium C of Sang (1956), and (ii) Medium C diluted to one-third normal strength of all constituents, except agar. It so happens that the two media reduce body size by about the same amount—some 25%—and while both considerably increase the larval period, the low-protein diet lengthens it more than the diluted medium does. In addition, two strains have been selected on the usual maize-meal medium, fortified with dried and seeded with live yeast. These were started at the same time and run in parallel. Evidence is also drawn from a short-term selection experiment on the live yeast medium, which was described in the preceding paper.

The selection procedure differed in one respect according to diet. For the two parallel strains on the live yeast medium, three pairs of flies were selected from each

of ten pairs from five replicate cultures, to make fifteen pairs chosen from a total of fifty pairs examined. On the aseptic media, an average of thirty pairs of flies were chosen each generation from about 130 pairs examined. This difference in population size—twice as great on the sterile media—was dictated by the need to collect sufficient eggs from the parent flies for an adequate series of aseptic cultures. Since these flies were reduced in size, their egg production was correspondingly lower. Unselected flies from the foundation population were regularly cultured for comparison with the flies grown on the live yeast medium. In addition unselected larvae were grown on the alternative aseptic media, while larvae from the strains selected on the sub-optimal diets were also grown on the ordinary medium, sufficiently often to see how the deviation from the performance of the unselected stock varied with diet.

3. RESULTS

(a) Selection on the live yeast medium

Figure 1 shows the response to selection in the pair of lines selected for large body size. They represent the same general features as quoted for the effects of mass selection in other populations (Robertson, 1955). The graph suggests that selection

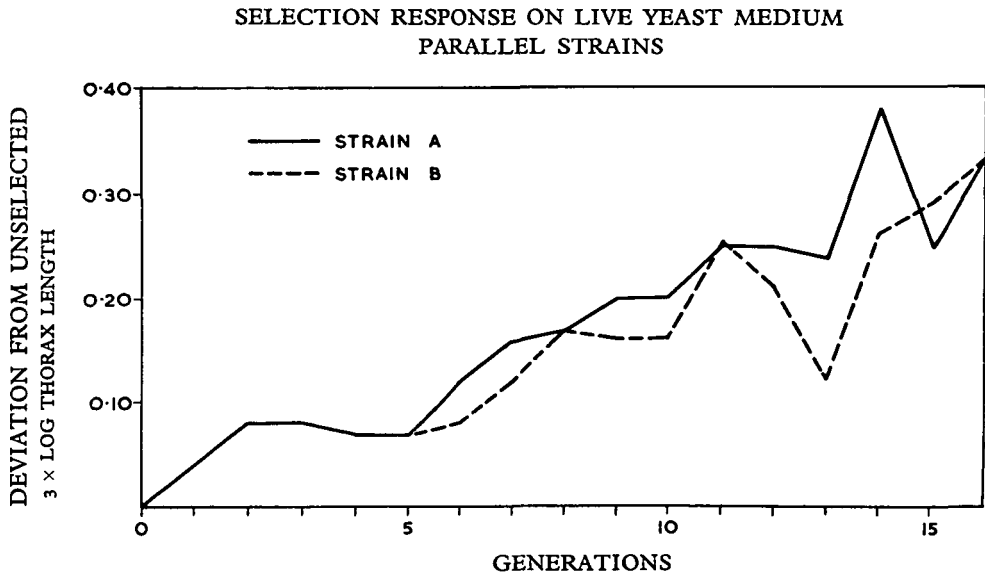SELECTION RESPONSE ON LIVE YEAST MEDIUM
PARALLEL STRAINS

Fig. 1. The two strains were selected for large body size on the ordinary live yeast medium. The average deviations from unselected were almost identical for the strains for the first five generations of selection.

was still effective after sixteen generations of selection when the experiments were discontinued. By this time the strains were some 30% bigger than the unselected flies. The general similarity of the selection response in the two lines, especially during the first five generations, is really quite remarkable.

(b) *Selection on the low-protein diet*

Figure 2 shows the selection response on the low-protein diet as deviations from unselected. Comparisons on both the aseptic and the live yeast medium are shown. On the low-protein diet, body size continued to change until generation 7 when progress ceased abruptly, and, apart from an unexplained decline at generation 9— almost certainly an artefact—the curve failed to rise appreciably during a further

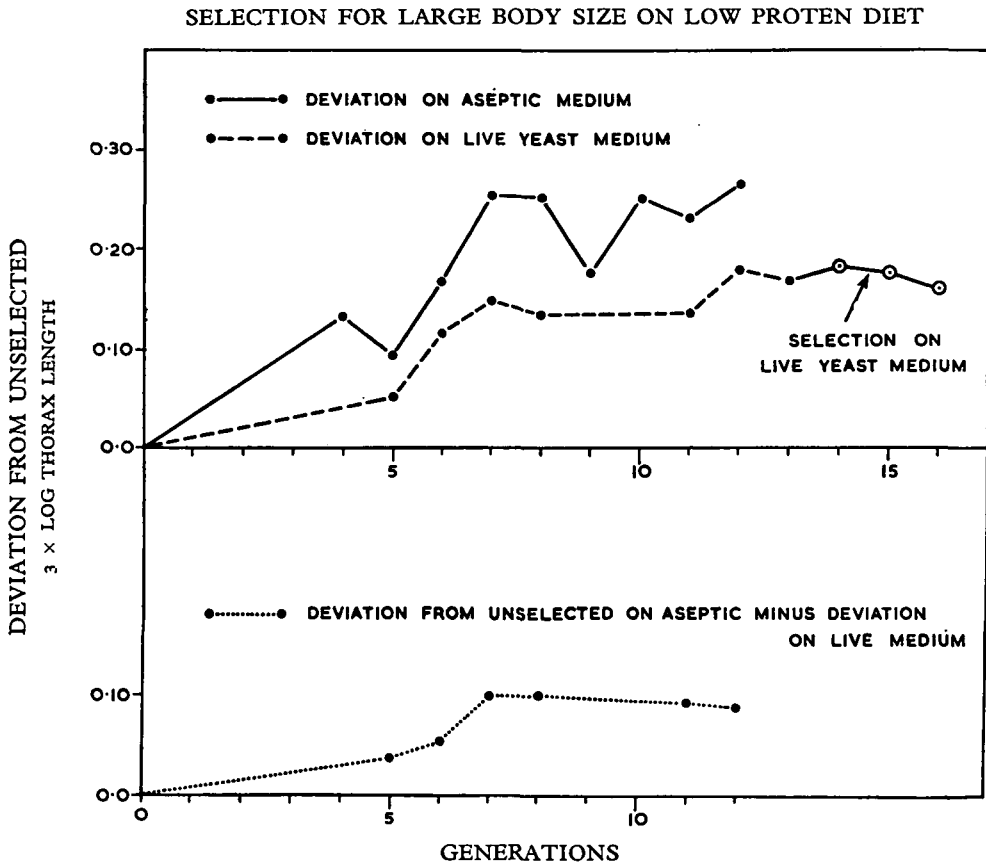SELECTION FOR LARGE BODY SIZE ON LOW PROTEN DIET

Fig. 2. The effects of selection on the synthetic, low-protein diet. After twelve generations selection was continued on the live yeast medium.

five generations, after which selection on the low-protein diet was discontinued. At generations 5 through 8 and also 11 and 12, progeny of the selected flies were also grown on the live yeast medium and their deviations from unselected are also shown.

Two features stand out. Firstly the deviation from unselected, on the log scale, is consistently less on the live yeast than on the low-protein diet. It appears that selection has picked out genotypes which are better adapted to the sub-optimal diet but which do not contribute to larger size on the favourable live yeast medium. The contribution of such effects to the total selection response can be estimated by subtracting the deviations from controls for the live yeast medium from the

corresponding deviations for the low-protein diet and such differences are shown in the lower graph of Fig. 2. Selection has improved performance on the low protein diet by some 10%. The rest of the response appears to be due to changes which are expressed on both low-protein and the live yeast media.

This result can be compared with the effects of growing large strains selected on live yeast medium on the same low-protein diet (Robertson, 1959, 1960). After a

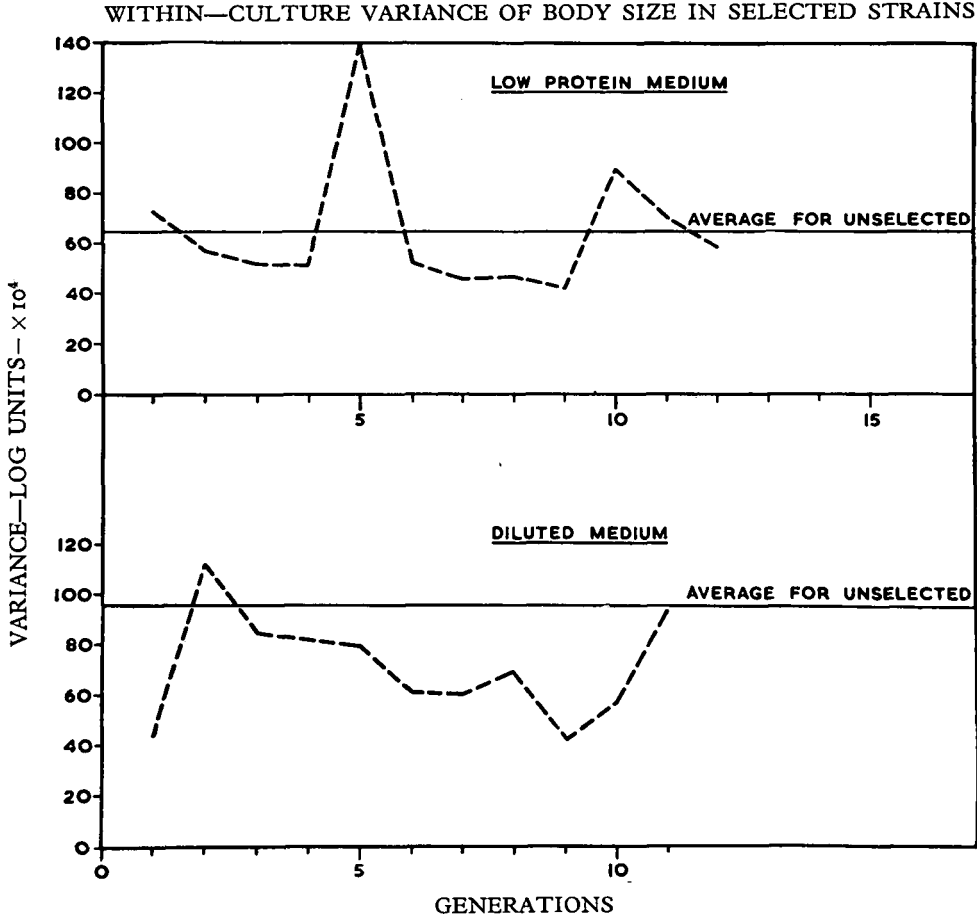WITHIN—CULTURE VARIANCE OF BODY SIZE IN SELECTED STRAINS

Fig. 3. The average within-culture variance for the unselected flies represents the pooled variance for the controls set up during the selection experiments together with data from other tests in which the same medium was used.

few generations, performance on the low-protein diet declines so that the deviation from unselected becomes less. Thus parallel selection for the same 'character'— body size—on different larval diets leads to different reactions to similar nutritional changes. It would be quite easy to produce large strains which deviate equally from unselected on the live yeast medium but which behave quite differently when the diet is altered.

The second notable feature of these results is the earliness with which the plateau

is reached—progress stops after only seven generations. In other mass selection experiments for large body size on the ordinary medium, the response extended over a longer period and attained a greater proportional increase over the foundation population (Robertson, 1955). Also, in the pair of lines selected from the Pacific population, selection response was much greater (Fig. 1). It is worth noting that the loss of variance due to restricted population size in successive generations should be greater, other things being equal, in the strains which responded most to selection, since there were only fifteen pairs of parents per generation, compared with thirty pairs on the aseptic medium.

The within-culture variance of body size tends to decline with effective selection on the low-protein diet. Figure 3 shows the variance in successive generations, compared with the average value for the wild population reared on the same medium. For the latter estimate, all available data have been combined, including data from tests not dealt with here. The variance declines over the first four generations or so and then remains fairly steady, apart from a jump at generation 6, which is probably due to infection of the synthetic cultures. This decline in variance is attributed to better adaptation to the sub-optimal diet which is accompanied by a reduction in the effects of segregation and recombination. The tendency for the variance to rise about the time the plateau is reached may be significant, and will be noted later.

Direct evidence for improved adaptation to the low-protein diet is provided by records of the duration of the larval period, which has been recorded at intervals; these are set out in Table 1.

Table 1. *Duration of the larval period of the strain selected on low protein*

| | Deviation from unselected—log days | |
| | Low-protein medium | Live yeast medium |
Generation		
4	− 0·06*	0·01
6	− 0·04*	0·01
8	− 0·11*	0·05
9	0·01	—
12	− 0·01	0·04*

Asterisks indicate significance at the 0·05 level of probability.

During the early period of selection, development time is significantly shortened in the strain selected on low protein. From the evidence given in the preceding paper, genetic changes which lead to larger body size and shorter duration of the larval period can only mean that growth is that much less affected by limiting factors in the diet. There is no evidence that such changes also shorten development time on the favourable medium, as might be expected, although there is some tendency for development time to be slightly increased at the end of the selection period, and this could imply some lowering of adaptation to the live yeast diet. On the low-protein medium, differences between selected and unselected in the larval period are later obliterated, due possibly to increasing importance of other kinds of change —characteristically expressed on the live yeast medium as well—which become

increasingly incompatible with the increase of body size via improved adaptation to the diet. If this is so, with suitable modifications of selection procedure, it might be possible to increase performance, and hence body size, on the low-protein diet to a higher level than was possible here; such changes might be expected either to leave average body size on the live yeast medium unchanged or to lower it. This point will be discussed again later in relation to the origin of the plateau on different media.

It could be argued that culture on the low-protein synthetic diet is a particularly effective way of revealing genetic differences so that selection would be relatively more discriminating and lead thereby to a greater rate of fixation which might contribute to an earlier fall-off in response, compared with the live yeast medium. It is true that there is a decline in variance, but there is every reason to attribute this primarily to qualitative change in the gene arrays rather than to increasing homozygosity. There is additional circumstantial evidence that different rates of fixation can hardly be invoked to account for these characteristic differences in selection response. It was noted that the level of egg production is strikingly higher in the selected than in the unselected strain. At generation 4, adult performance of selected and unselected flies reared on the low-protein medium was recorded over the 4 days of peak production, while at this and also the fifth and seventh generations, the performance of flies grown on the live yeast medium was recorded. In the test at generation 4, for larvae grown on low protein, the selected flies laid some 30% more eggs than the unselected, over the test period—a highly significant difference. Part of this difference could be attributed to the improved adaptation to the sub-optimal diet, discussed above, which had become effectively less sub-optimal for them than for the controls. This would naturally result in higher egg production, since variation in body size due to larval nutrition is highly correlated with the rate of egg production (Robertson, 1957). But a difference of this magnitude suggests that intrinsic egg production was also higher, and this was confirmed in the three comparisons between selected and unselected flies grown on the ordinary medium. Here the selected flies laid some 15% more eggs—again, statistically, a highly significant difference. It is well known that egg production is sensitive to loss of heterozygosity, and if selection on the synthetic media had contributed appreciably to the level of inbreeding, we should hardly expect egg production to increase. How far this striking correlated response is peculiar to the conditions in which selection was carried out, is not yet clear and provides material for further study. Finally it is worth noting that records of viability from egg to adult showed little evidence of change and certainly no decline in the selected strains.

Hence the early plateau on the low-protein diet is essentially due to incompatibility between alternative effects which promote larger body size by different kinds of change in growth and metabolism. At first, such different effects may behave more or less independently, in contributing to selection response, but a few generations of selection create a situation in which potential increase in body size in one way involves changes which would reduce it in other ways and so the response stops, since body size is the sole criterion of selection. This interpretation does not conflict with the earlier evidence that selection, for the kinds of effect which are expressed

on the live yeast medium, is associated with greater proportional reduction on low protein diets.

It could be argued that if the strains selected on low protein were transferred to the favourable, live yeast medium, the physiological incompatibility would no longer exist, since the genetic changes which improve performance on the low-protein diet would be irrelevant under these conditions. The potential reserves of genetic variation, which lead to larger body size on the live yeast medium, would become accessible and allow selection to continue. To test this, after generation 12 selection was carried out on the live medium for a further four generations. No increase in size occurred beyond the level characteristic for this medium during the plateau period. It may be inferred that the genetic changes effected by selection on low protein are not neutral with respect to growth on the live yeast medium. Either they inhibit the expression of genetic differences which otherwise would contribute to the variance, or, and perhaps more likely, selection on the low-protein diet has lowered adaptation to the live yeast medium and established the conditions for mutual incompatibility between alternative pathways which promote larger body size. To realize the potential reserves of variation it would be necessary to recreate the right conditions. This would involve undoing the work of selection on the low-protein diet, which would entail a reduction of body size before selection could be re-established with some prospect of reaching the levels found in strains selected from the beginning on the ordinary medium.

(c) *Selection on the diluted medium*

Selection procedure on this medium was identical with that for the low-protein diet. Figure 4 shows the steady response until generation 8, when progress ceased
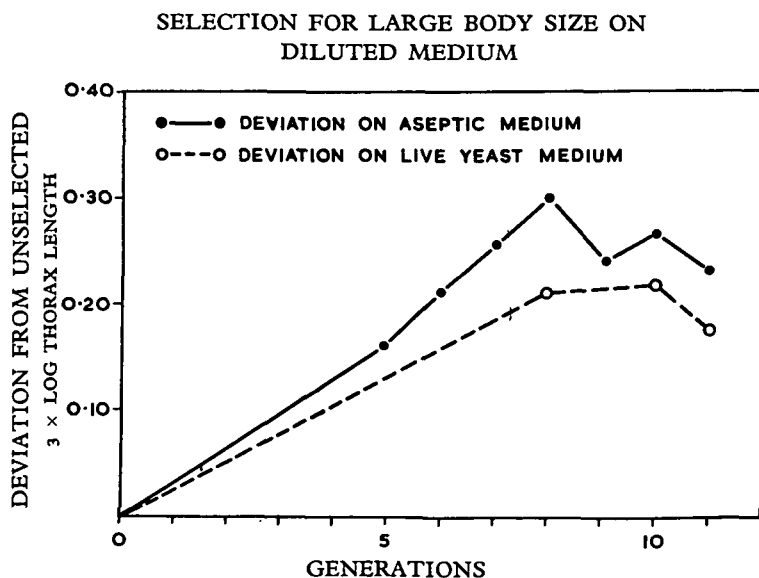

Fig. 4. The effects of selection on the synthetic, diluted medium.

and the strain thereafter fluctuated about a level equivalent to 0·25 log units above unselected. Thus the selection response here is very similar to that on low protein, both with respect to the level of the plateau and the number of generations required to reach it. There is a difference, however, in that the deviation from unselected on the live yeast medium is relatively greater than in the other line. The within-culture variance also declines with selection and shows a tendency to rise after the plateau has been established. Thus the two separate tests on qualitatively different sub-optimal diets present essentially the same pattern of response.

(d) Heritability estimates

Since we have now the response to selection for large body size in three different environments, we can compare the estimates of heritability. As the deviations from controls were not scored for the first few generations on the diluted medium, the data from generations 5, 6 and 7 for all lines are used for the estimates. Response to selection is taken as the average deviation from unselected for these three generations on the medium used in the selection. Heritability is estimated from the ratio of response to cumulated selection differential (Woolf; see Falconer, 1955); the estimates have been averaged for the three generations in question. The cumulated selection differential is simply the sum of the average deviations of selected flies from their culture means for the preceding generations of selection, i.e. it refers to the total selection pressure applied up to the generation in question. For the live yeast medium, the estimate quoted in Table 2 refers to the average of the values from three large strains—the two selected in parallel and also the large strain used in the experiments described in the first paper of this series. Table 2 shows the various comparisons.

Table 2. *Heritability on different media*

Medium	Deviation from unselected	Cumulated selection differential	Heritability
Live yeast	0·102	0·343	0·30
Low protein	0·176	0·504	0·35
Diluted	0·209	0·548	0·38

The selection response, in terms of deviation from unselected, is greatest on the diluted medium and least on the live yeast. But the cumulated selection differential is least in the latter and considerably greater on both the sub-optimal media, reflecting the greater within-culture variance which has been noted earlier. The heritability estimates are quite similar for the three comparisons. Whether or not this means that sub-optimal conditions also inflate the developmental variance remains to be seen and this possibility is being studied in further tests. It is equally possible that the relative contributions of additive versus non-additive effects also vary according to diet. The fact remains that the similarity between the estimates of heritability does not also apply to the subsequent performance of the strains. On the live yeast medium the predictive value is high, while on the other media it is nil,

since the response to selection ceased immediately after the generations to which these estimates apply.

(e) *Genetic correlation*

Falconer (1952) has discussed the problem of how to handle the relations between the response to selection for the same 'character', say body size, in two different environments, such as high and low planes of nutrition, and the expression of the differences due to selection when each strain is reared in the environment other than that used for its selection. Thus for each treatment we have a measure of the direct response and a correlated response from the performance of the strains selected in the alternative conditions. This so-called correlated response can be treated formally as a case of genetic correlation which can be estimated from the equation:

$$r_G = \frac{\text{correlated response}}{\text{direct response}} \cdot \frac{h_1}{h_2} \cdot \frac{i_1}{i_2},$$

where h_1 and h_2 refer to the square roots of the heritabilities on the alternative conditions; h_1^2 is the heritability in the environment in which the direct response is measured. i_1 and i_2 represent the corresponding estimates of selection intensity, namely the average selection differential divided by the average within-culture standard deviation. For each set of comparisons there are two estimates of genetic correlation which should agree if the assumptions which underlie this statistical procedure are valid.

The present experiments provide sufficient data for such estimates. The heritabilities are the same as those quoted in Table 2. The strain reported on in the preceding paper has been used to provide records of performance on sub-optimal diets of a large strain selected on live yeast. Tests on alternative media were carried out during selection and, for the low-protein medium, the data from tests after 4, 6 and 7 generations of selection have been averaged. For performance of this strain on the diluted medium we have only one comparison, at generation 7. For the strain selected on low protein, performance on the live yeast medium is represented by the average of the values recorded for generations 5 to 7. For the strain selected on diluted medium, corresponding values have been estimated from Fig. 4.

Table 3 shows the values used in the estimation of the genetic correlations. There is a considerable lack of consistency between the alternative estimates. Since the heritabilities and the average selection differentials are rather similar for the different strains, the discrepancies are due to the characteristic differences in the growth of the different strains on the alternative media. In all cases the deviation from unselected is less on the alternative medium which is used to estimate the correlated response. This difference is specially striking when the strain selected on live yeast is grown on the diluted medium.

It is worth noting that these discrepancies arose after only a few generations of mass selection. There is evidently little prospect of reliable extrapolation from past to future performance since the computed values of the 'genetic correlation' will vary rather violently in successive generations of selection. Thus, in the first few

generations of selection on the live yeast medium, culture on low protein makes little difference to the proportional deviation from unselected. This was noted in the preceding paper (Robertson, 1960). But as selection proceeds, a substantial deviation may be converted into a low, zero or possibly, even a negative deviation on sub-optimal diets. Such apparent contradictions in the estimates of genetic correlation are to be expected if selection for the same 'character' under dissimilar environmental conditions involves qualitatively different changes in growth which

Table 3. *Correlated response on different media, deviations from unselected, log units*

	Media		
	Live yeast	Low protein	Diluted
Direct response	0·10	0·17	0·21
Correlated response			
Live yeast	—	0·08	0·02
Low protein	0·11	—	—
Diluted	0·16	—	—
h	0·57	0·59	0·62
i	7·61	6·70	6·40
r_G		1·15	1·70
		0·45	0·09

lead to characteristic differences in reaction when the environment is altered in a particular way. The practical utility of the statistical procedure is open to question if it has such low predictive value and confounds relevant biological differences in a single numerical score.

4. DISCUSSION

These experiments support the view that different nutritional conditions during growth bring different gene arrays into prominence. Although adult body size may be the single criterion of selection, individual variation in different conditions represents, to greater or lesser degree, the effects of genetic segregation and recombination on different processes of growth and metabolism. Hence when environmental conditions are sufficiently different, it is misleading to refer to the 'character' body size as if it were a kind of ultimate category. By suitable control of the environment, selection can be used systematically as a tool to alter growth in different ways. By including records of development time, the reaction to controlled differences in diet and any other criteria which turn out to be relevant, genetic variation in body size, which at first appears amenable only to statistical description and analysis, can be studied in new ways in which genetic behaviour and physiological effect are considered together.

On the sub-optimal diets used here, part of the response to selection for larger body size represents improved adaptation to these conditions. Direct support for this view is provided by the decline of the within-culture variance during the early stages of selection, the shorter development time and also the higher egg production

of the low-protein strain when compared with unselected flies grown on the same medium. On the other hand, there is no evidence in these nor in any other experiments to suggest that selection for larger body size on the live yeast medium represents better adaptation to such conditions. Such differences in the kinds of change which accompany ostensibly parallel selection in different environments are obviously related to differences in how far selection can change the phenotype.

If apparently similar increases of body size can depend on different modifications of growth, it is unlikely that the possibility of substantial change in one direction will be independent of changes in other possible directions. In particular, it was suggested that continued improvement in adaptation to the sub-optimal diets soon becomes incompatible with further change of the kind normally selected for on the live yeast medium, but which also contributes to the variation of body size on the sub-optimal diets. This is consistent with the later rise in the within-culture variance after the period of steady decline, since selection may finally result in some loss of adaptation to the sub-optimal diet and so lead to greater evidence of genetic segregation. The so-called plateau originates when alternative ways of increasing body size, which are initially more or less independent in action, become negatively correlated in effect. The nature of the diet largely determines how far body size can be increased before the impasse is reached. A more extensive comparative study of selection response on different diets would be instructive, since it should throw light on the conditions and selection procedure, for a given population size, best suited for sustained response. It would be rather surprising if the results of uncritical selection for large body size on the live yeast medium could not be improved upon with a better understanding of how growth may be altered in different ways to produce apparently similar variation in final size.

When the strain which had ceased to respond on the low protein was transferred to the live yeast medium, body size did not increase with further selection and remained well below the level reached by strains selected on the live yeast medium. It can hardly be accepted that seven generations of mass selection, with double the population size, will have exhausted the genetic variation which normally contributes to the response under favourable conditions. The apparent contradiction probably rests on the fact that selection on the sub-optimal diet has created a new genetic situation in which it is impossible to gauge the amount of further progress from the performance of strains selected on the live yeast medium from the beginning. Possibly selection on the sub-optimal diet has lowered performance on the live medium and potential variation which favours larger size could only be exploited by undoing the work of selection on the other media.

It is known from other experiments (Robertson, 1959, 1960) that selection for larger body size on the live yeast medium entails, sooner or later, relatively greater reduction in body size—compared with unselected flies—when larvae are grown on protein-deficient or diluted media. It might be argued that a genetically controlled tendency to attain larger body size would automatically raise the protein requirements above the level required for smaller strains. However, such a simple explanation will not do. *A priori* there is no reason why the larval period should not be

extended under such adverse conditions, so that the proportional decline in body size remains the same. Also, strains selected for smaller body size may decline relatively more on sub-optimal diets as well. So it rather looks as if adaptation to the specific composition of the diet, such as amino-acid balance for example, may be relatively more important than crude differences in protein content. This problem will require further study since it suggests ways of defining the essential features and more important limiting factors in the nutritional conditions to which the species is adapted. These considerations must be borne in mind when the response to selection for the same character is being compared in populations adapted to different conditions, and this will be especially true of comparisons between species. Observed differences in the pattern of response may be thought to depend on purely genetic causes such as linkage relations or chromosome number when in fact they stem from unequal differences between the conditions in which selection is practised and those in which the animals normally live.

These experiments suggest that *Drosophila* does not follow the rules formulated by Hammond (1947) with respect to the selection of livestock on high or low planes of nutrition. Naturally direct extrapolation from the growth of an insect to that of a mammal may be unwarranted; nevertheless, certain general observations are worth noting. It is true that selection on a high plane of nutrition has so far led to the greater absolute response to selection for large body size, but the difference due to selection is not maintained when the animals are grown on a low plane. Also, differences produced by selection on a poor diet are proportionally less when the diet is improved, while adaptation to the low-plane conditions may reduce the possibility of increasing body size by further selection under better conditions. The rather crude term 'plane of nutrition' can be a source of confusion, since it rather implies that nutrition can be graded on a continuous quantitative scale. Although the gross food intake can be varied quantitatively, qualitative differences in the factors which limit growth are bound to occur on different 'planes', and thus provide a basis for the selection of gene combinations which affect metabolism in different ways.

From the characteristic differences in selection response, I have inferred that selection on different diets alters growth and metabolism in different ways. By comparing the growth of these strains on different controlled diets it should be possible to test this inference directly. The next paper in this series will take up this problem.

SUMMARY

1. Strains from a cage population of *Drosophila melanogaster* were selected for increased body size on the live yeast medium and on two aseptic synthetic media, (1) deficient in protein and (2) with all nutrients reduced to one-third the normal concentration required for growth to normal size. Both these media reduce body size by about 25%.

2. In two strains, mass selected on the live yeast medium, the response continued fairly steadily for at least sixteen generations, when the experiment was discontinued. By this time body size had been increased by some 30%.

3. On the sub-optimal diets the number of selected parents per generation was twice as great as on the live yeast medium, for technical reasons, but the response ceased abruptly after seven or eight generations of selection at a level considerably below that attained by the strains selected on the more favourable diet. Also, when selection was continued on the live yeast diet, no further progress occurred.

4. Flies selected on the different diets and also unselected flies have been grown on the alternative conditions to see how the deviation from unselected is affected. For both strains selected on sub-optimal diets, the deviation from unselected is appreciably greater on the medium used for selection than on the live yeast medium.

5. The response to selection for larger body size on deficient diets can be attributed partly to better adaptation to these conditions. This inference is supported by several lines of evidence. The within-culture variance, which is clearly greater when selected flies are grown on deficient diets, declines with effective selection. Also in the low-protein strain, for which data are available, the duration of the larval period is shortened in the early stages of selection, while egg production considerably exceeds that of unselected flies grown on the same diet.

6. Other effects, of the kind normally selected for on the live yeast medium, also contribute to the variation and selection response on the deficient diets. At first they appear to act more or less independently of the genetic changes which favour increased size via improved adaptation to the diet, but continued selection soon leads to mutual incompatibility between the alternative pathways in growth. Since no further progress occurred when selection was continued on the live yeast medium, the earlier selection had probably lowered the level of adaptation to the live yeast medium. A new genetic situation had been created in which it was impossible to gauge the amount of further progress by reference to the behaviour of strains selected on the live yeast medium from the beginning.

7. Estimates of heritability, based on cumulated selection differentials, are rather similar in the different diets and range between 0·30 and 0·38. On the live yeast medium, the estimate provides a fair guide to future progress, whereas, on the deficient diets, the predictive value is nil since response ceases immediately after the generations which provide the data for the estimates.

8. By comparing the deviation from unselected on the media used for selection and also the other media, alternative estimates of genetic correlation in performance in different conditions can be computed. The estimates were sufficiently divergent to cast doubt on the practical utility of the statistical procedure, which takes no account of the likelihood that individual variation in body size in different environment represents to greater or lesser degree the effects of segregation on different processes of growth and metabolism.

9. Since the course of selection is influenced by nutritional conditions, comparisons of response to selection for the same 'character' such as body size, in populations or species adapted to different conditions, must allow for the likelihood that unequal differences between the conditions in which selection is carried out and those in which the animal normally lives may be an important cause of differences in response.

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