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Genetic analysis of larval feeding behaviour in *Drosophila melanogaster*

II. Growth relations and competition between selected lines

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SUMMARY

Growth relations of lines selected for fast or slow larval feeding rate have been compared with those in the genetically heterogeneous control base population from which they were derived. Larvae of the slow strain have reduced growth rate and reach their critical weight for pupation later than unselected larvae. Larvae of the fast strain attain their critical weight at the same time as the unselected control larvae, suggesting that growth rate in the precritical period of development is already maximized in the base population and cannot be improved by increasing food intake. This constraint does not apply to the fixed period of post-critical growth however, since fast feeding larvae give rise to larger adult flies than the controls.

Larval feeding rate is affected by genes located on all three major chromosomes. The small fourth chromosome has negligible effect. Selection for slow feeding rate has led to an increase in the frequency of recessive genes affecting the character. High scores of larvae selected for fast feeding rate depend upon interactions between non-homologous selected chromosomes which individually have little effect. Larval feeding rate in the control unselected population appears to be buffered, firstly by epistatic interactions against the effects of chromosomes tending to promote 'supra-optimal' feeding rate and, secondly, by dominance against chromosomes promoting a lowering of feeding rate.

Under conditions of scramble type competition between the selected lines for limited resources, fast feeding larvae have a higher survival rate, and complete their period of larval development earlier to give larger adult flies than their slow feeding competitors. The contribution of larval feeding rate to competitive ability at different levels is discussed, and it is suggested that the effects of change in this behavioural character may be far reaching.

1. INTRODUCTION

Drosophila melanogaster females do not regulate the number of eggs laid, so that the larval population tends to overcrowd the food medium leading to competition between them for the available resources. Competition, as defined by Birch (1957),

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occurs when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one another in the process. The simplest form of competition is the scramble type (Nicholson, 1955), in which individuals exploit the same limited and necessary resource, each individual obtaining a share of that resource in proportion to its competitive ability. Competition for food between *D. melanogaster* larvae tends to be of this kind. Bakker (1961, 1969) has made a thorough study of the factors which determine success in competition for food among larvae, arguing that differences in the rate of larval feeding are likely to have an important bearing on its outcome. Kearsey (1965) also suggested that differences in competitive ability between larvae depend on feeding rate, although it is possible to avoid the suggestion in this instance as no account was taken of possible differences in growth rate between the competing genotypes. More recently Sewell, Burnet & Connolly (1975) produced strains of *D. melanogaster* differing in larval feeding activity by selecting for differences in the cephalopharyngeal retraction rate. The genetic basis of the differences between the selected strains is examined here, together with an analysis of the effects of feeding rate on larval growth relations and competitive ability.

2. MATERIALS AND METHODS

A description of the procedures used for the measurement of larval feeding rate is given by Sewell, Burnet & Connolly (1975). The strains used for the investigation described here are the Fast A and Slow A strains produced by these authors. The stocks have been subjected to approximately equivalent levels of inbreeding and selection since their origin from the control base population.

Studies on larval growth relations were made by allowing 3 day old females to oviposit for a 2 h period on 5 cm diam. watch glasses filled with water agar overlaid by a lawn of fresh live baker's yeast. First instar larvae were transferred as they hatched from the egg to freshly yeasted watch glasses at a constant density of 50 larvae per watch glass, and enclosed in a Petri dish. Fresh yeast additions were made daily. This procedure allows individual larvae to be easily located and removed from the yeast when required. At 4 h intervals larvae were picked off the medium, rinsed, lightly surface dried by rolling on absorbent tissue, and weighed. They were then transferred to 5×1 in. glass vials containing water agar gel, without nutrients, to complete their development. The critical weight was computed from an analysis of the regression of the percentage of larvae pupating (transformed to probits) on larval body weight (in logarithms). A complete account of the method of probit regression analysis used is given by Finney (1962).

The effects of selected chromosomes in heterozygous condition were tested by crossing males from each selected line (F and S) separately to females of a control unselected *yellow*; *brown*; *scarlet* stock. F_1 males were then backcrossed to virgin females from the parental marker stock. 70 h old larvae from the backcross were scored for larval feeding rate and transferred to individual feeding vials to complete

their development so that the adult morphological markers could then be scored. Larval feeding rate scores for the first 25 flies from each of the eight genotype groups were then used for the analysis. The effects of selected chromosomes in homozygous condition were tested by creating the eight possible homozygous combinations of control and selected chromosomes, using the balancer chromosomes In(2LR)SM5, *al*^{2}*Cy lt*^{v} *cn*^{2} *sp*^{2}, and In(3LR)TM3, *y*$^{+}$ *ri p*^{p} *sep bx*^{34e} *e*^{s}, and the marker chromosomes *Bl L* and *Sb*. No balancer was needed for the *X*-chromosome in the crossing scheme employed. The segregation of the *Y* and fourth chromosome was not controlled. Fifty 70 h old larvae of mixed sexes from each of the eight genotype groups were scored for feeding rate.

The strains F *spa* and S *spa* were synthesized from the respective fast and slow selected lines by crossing to the stock *sc*^{sl} *B In S w*^{a} *sc*^{s}*;* In SM1 *al*^{2} *Cy sp*^{2}*/dp b Pm ds*^{33k}*; C Sb/Ubx*^{130} *e*^{s}*; spa*^{pol}. Heterozygotes for the three inversion-containing balancer chromosomes were intercrossed, and the derived subline homozygous for each of the three major chromosomes of the selected line and the fourth chromosome marked with *sparkling* was scored for larval feeding rate at 70 h together with the corresponding parent selected line. No significant differences in feeding rate between F and F*spa*, or between S and S*spa*, were found. From this it was concluded that the fourth chromosome makes a negligible contribution to the variation in feeding rate and no further account was taken of this chromosome.

Larval competition experiments were carried out using 3 × 1 in. glass vials containing 5 ml of a 2 % water agar gel over which was placed freshly made live baker's yeast. The yeast was layered onto the agar as a thick suspension in measured quantities to give yeast fresh weight equivalents of 50, 100 and 200 mg respectively. First-instar larvae were inoculated into test cultures at a constant density of 50 larvae of each competing strain, that is an overall density of 100 larvae per culture. Care was taken to avoid any initial differences in age between competing larvae: synchronized first-instar larvae were inoculated into the competition cultures together, at the time of eclosion from the egg. Development rate was determined by counting the number of adults at daily intervals. The adult flies collected at eclosion were killed and stored in a refrigerator in small sealed polythene specimen tubes. They were subsequently weighed after a standard period of equilibration to room temperature.

All experiments were carried out at 25 ± 1 °C under a constant schedule of 16 h light, 8 h darkness.

3. RESULTS

(i) *Larval feeding rate*

Larval feeding involves scooping or rasping with the chitinous mouth hooks. The semi-liquid food medium is ingested by a pumping action of the muscular pharynx. As far as can be ascertained by direct observation, movements of the pharynx and cephalopharyngeal sclerites, which actuate the mouth hooks, are coordinated so that the scooping and pumping actions are made together. Conse-

quently the retraction rate of the sclerites, visible through the translucent head region, is an indicator of the rate at which the pharyngeal pump is operating. Apparently, the actions of pumping and scooping can be uncoupled. Occasionally a stationary larva has been observed with its mouth hooks embedded motionless in the substrate with the pharyngeal pump continuing to operate as indicated by the entry of suspended food particles into the pharynx. This of course suggests the possibility that differences in the rates of cephalopharyngeal retraction in larvae

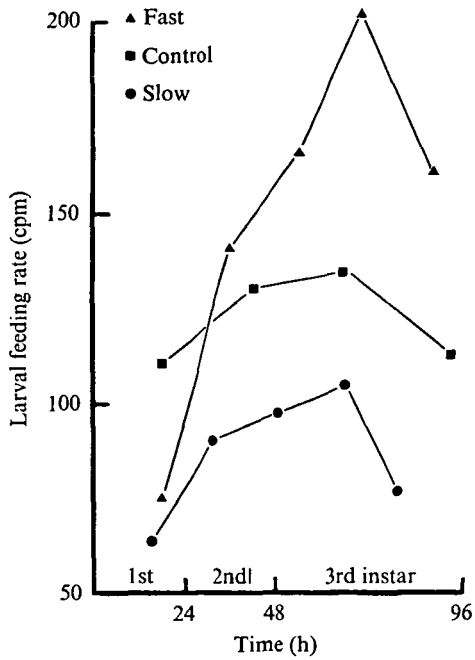

Fig. 1. Feeding rate measured as the number of cephalopharyngeal retractions/min. in larvae of the fast and slow selected lines. To facilitate comparison of means at the same physiological age the data for each strain are shown on a standardized larval period of 96 h.

of the selected lines may represent only a change in the rate of scooping without a corresponding change in the action of the pump, so that there is no net difference in the rate of food acquisition. A check against this possibility was made by comparing the throughput of food in fast and slow feeding larvae of the two selected strains. Larvae were cultured initially on a yeast suspension containing finely divided charcoal to blacken the food. They were then washed rapidly and transferred to a yeast suspension without charcoal. The opaque gut contents are visible through the body wall and the time taken to clear the gut can be measured directly. A comparison of second instar larvae of similar physiological age showed that larvae of the slow feeding stock take longer to effect gut clearance than fast feeding larvae, indicating that differences in cephalopharnygeal retraction rate, in this instance, reflect real differences in the rates of food acquisition.

The rate of cephalopharyngeal scooping is age related. There is a sustained increase in feeding rate during the first and second instars to a maximum reached during the first half of the third instar. The rate declines during the second half of the third instar and feeding ceases altogether when the mature larva moves across the surface or out of the food medium in search of a suitable pupation site.

As shown in Fig. 1, feeding rate in the fast selected line is consistently higher than in the slow line throughout the larval period. The difference between the lines is smallest during the first instar when larvae of the fast line actually have a lower feeding rate than the controls. In the fast line feeding rate more than doubles in the period up to the middle of the third instar whereas the slow line shows a smaller proportional increase over the same period. The feeding rate in the fast line is nearly twice that in the slow line by the time the larvae are entering their critical period.

(ii) *Growth relations in the selected larvae*

The larvae of *D. melanogaster* must reach a minimum body weight before they acquire the capability of pupating. This minimum or critical weight is reached early in the third instar (Bakker, 1961; Robertson, 1963; Church & Robertson, 1966). The duration of the pre-critical period for larval growth can be greatly

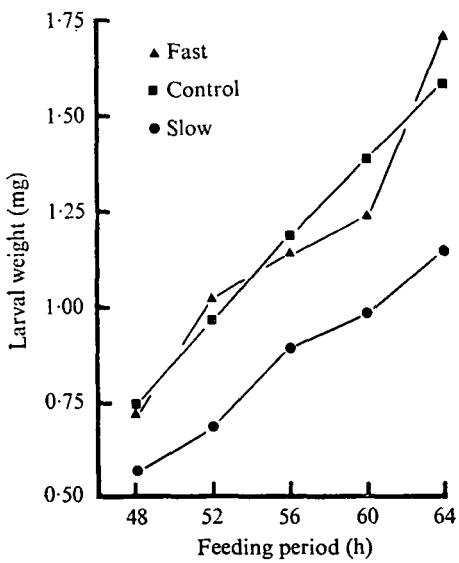

Fig. 2

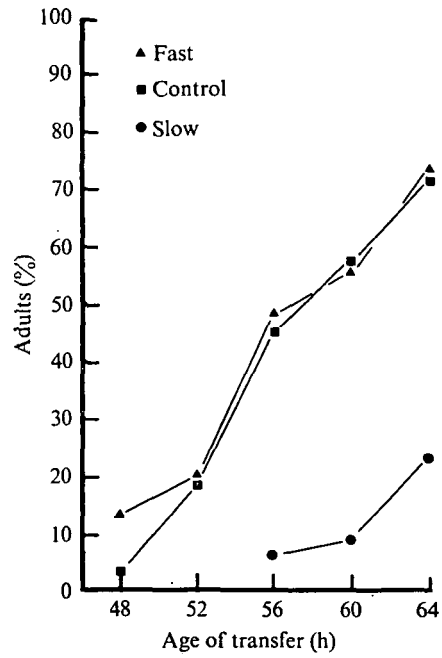

Fig. 3

Fig. 2. Weight gain (mg) in larvae of the fast and slow selected lines, and for the control unselected base population, during the first part of the third larval instar.

Fig. 3. Mean percentage of larvae capable of pupating to hatch as viable adults following removal from the food medium at successively later time intervals after eclosion from the egg.

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extended when nutritional conditions are suboptimal, but, when the critical weight is reached there appears to be a decisive shift in hormonal relations, leading to a fixed period for post-critical growth to pupation. The critical weight together with the growth rate of the larva in the post-critical period determines the body weight of the imaginal fly (Robertson, 1963; Church & Robertson, 1966). The significance of these facts for the outcome of competition between larvae differing in feeding rate is that, under conditions of competition for limited resources, ability to survive will depend on larvae being able to achieve their critical weight before the food supply gives out. However, genotypes with a lower critical weight requirement are, *ceteris paribus*, likely to enjoy a competitive advantage, in terms of larval survival rate, over other genotypes with a higher critical weight to reach. The effects of such a difference in growth relations, if undetected, could obviously be confounded with those resulting from differences in feeding rate between genotypes.

Table 1. *Mean body weight (mg) at the critical point for pupation in larvae of the fast and slow feeding lines*

	Critical weight (mg)	Confidence interval 95 %
Slow	1·24	1·16–1·32
Fast	1·21	1·15–1·27

Fig. 2 shows the gain in body weight for selected lines under optimal conditions of food supply in the period in which they reach their respective critical weights. Larvae of the fast feeding line increased in weight at a significantly higher rate and are considerably heavier than the slow feeders. The mean critical weight, measured as the weight at which 50 % of the larval population is capable of pupating successfully, is closely similar in the two selected lines (Table 1). Although there is no significant difference between the fast and slow feeding lines in the critical weights they have to attain, the fast feeding larvae reach their critical weight for adult eclosion earlier than the slow feeding larvae, as shown in Fig. 3.

Larvae of the fast selected strain show a substantial advantage over the slow strain with respect to growth rate and the speed at which they reach their critical weight, but contrary to what might be expected, they have no such advantage over larvae from the control base population. As shown in Figs. 2 and 3, the fast and control strains are closely similar in their growth rates, and reach their critical weights at the same time. Evidently growth rate in the precritical period of larval growth is already maximized and cannot be improved by an increased rate of food intake. This constraint does not seem to apply to the post-critical growth phase since adult flies of the fast feeding strain are some 7 % heavier in body weight than the corresponding control flies.

(iii) *Genetic analysis of the selected lines*

Some insight into the genetic organization of feeding rate in larvae can be obtained by exchanging intact chromosomes between a given selected line and a

control unselected strain. Substitution, singly or jointly, of selected chromosomes in heterozygous and in homozygous condition into an otherwise control unselected background can be used to test for additivity and dominance, and to detect epistatic interaction between genes located on different chromosomes. Ideally this involves synthesizing all (27 female, 18 male) combinations of chromosomes from any two strains being compared (see Robertson, 1954; Kearsey & Kojima, 1967), but practical considerations surrounding the management of behavioural assays on precisely timed material make it advisable first to undertake a more limited investigation in order to see whether a full scale analysis would be worth while. The results of such an analysis are shown in Table 2.

Table 2. *Comparison of the effect on larval feeding rate of heterozygous and homozygous substitutions of selected chromosomes into the genetic background of an unselected control strain. The effects are in each case expressed as the deviation (retractions/min.) from the homozygous unselected control*

	Slow		Fast	
Chromosome	Heterozygous	Homozygous	Heterozygous	Homozygous
1	−3·82	−11·9**	2·42	−9·8**
2	−1·63	−32·4**	0·19	−10·3**
3	3·45*	−35·5**	1·07	0·6
1+2	−3·0	−40·5**	4·4*	28·5**
1+3	0·5	−34·7**	6·0*	−5·3
2+3	−11·9**	−29·4**	17·3**	20·1**
1+2+3	−17·1**	−65·3**	26·1**	58·6**

* and ** denote deviations which are significant at the 5% and 1% levels of probability, respectively.

We are clearly dealing with a highly non-additive situation. There is substantial aggregate dominance of unselected chromosomes over slow chromosomes, indicated by the fact that substitution in heterozygous condition of chromosome 1S, 2S or 3S into an otherwise unselected background has very little effect compared with the corresponding homozygous substitution. Single substitution of fast chromosomes in heterozygous condition also has very little effect, whilst the homozygous substitution of chromosomes 1F and 2F, in each case, actually causes a significant reduction in feeding rate. It is where chromosome 2F is associated with at least one other chromosome from the selected line that we observe a significant increase in feeding rate.

The effects of single or joint substitution of selected chromosomes have been analysed using a separate 2^3 analysis of variance for each set of eight genotype groups representing different combinations of chromosomes in heterozygous condition, and similarly for each set of combinations in homozygous condition. A summary of the results of these analyses is presented in Table 3.

Each of the three slow chromosomes has a significant effect in heterozygous condition of reducing feeding rate, and there is interaction between chromosomes

2S and 3S. The numerical values for the components themselves show that the deviation of the triple heterozygote (S/C; S/C; S/C) is largely accounted for by the effect of chromosome 2S and interaction between 2S and 3S. Each slow chromosome in homozygous condition has a significant effect in reducing feeding rate. Although there are interactions between each of the homozygous slow chromosomes these are not uniform in direction, since interaction between homozygous chromosomes 2S and 3S is in the direction of the unselected control and opposite in sign to the joint effects of these chromosomes in heterozygous condition.

Table 3. *Significant main effects and interactions for selected chromosomes. The direction of the effect for each component is indicated as* (+) *increase or* (−) *decrease in feeding rate score*

	Slow		Fast	
	Heterozygous	Homozygous	Heterozygous	Homozygous
Main effects				
Chromosome 1	−*	−**	+**	+**
Chromosome 2	−**	−**	+**	+**
Chromosome 3	−*	−**	+**	+**
Interactions				
1 × 2	.	−**	.	+**
1 × 3	.	−**	.	.
2 × 3	−**	+**	+**	+**
1 × 2 × 3	.	−**	.	.

* and ** denote significance at the 5% and 1% levels, respectively.

Each of the three major chromosomes from the fast feeding selected line increases larval feeding rate in heterozygotes, and there is a strong interaction between chromosomes 2F and 3F in the direction of selection. The picture is similar for homozygous chromosome combinations with interactions in the same direction between 1F and 2F, as well as 2F and 3F, towards faster feeding rate.

Genes controlling larval feeding rate are evidently located on each of the three major chromosomes of *D. melanogaster*.

Selection for slow feeding rate has led to an increase in the frequency of recessive genes affecting the character. The control unselected chromosomes show aggregate dominance for control feeding rate over the selected slow chromosomes, but the pattern of interchromosomal interactions also suggests a degree of interaction between unlinked gene loci. Interchromosomal interactions are even more striking in the fast selected line. The analyses of variance in Table 3, based on average effects, indicate that each of the fast selected chromosomes has a significant effect but we can see, from Table 2, that in fact no individual chromosome alone from the fast selected line, either in heterozygous or in homozygous condition, significantly raises feeding rate in an otherwise unselected genetic background. Joint substitution of at least two non-homologous selected chromosomes is required to achieve any significant increase in feeding rate over the control level. A possible inference is, that larval feeding rate in the control unselected population is buffered

by epistatic interaction against the effects of genic imbalance in any chromosome tending to promote supra-optimal feeding rate.

(iv) *The effect of feeding rate on the outcome of competition*

The conditions for scramble type competition were created by presenting equal numbers of two competing genotypes with a known initial quantity of fresh yeast representing a fixed and non-renewable food supply. Three yeast levels were chosen: (i) 200 mg corresponding to an *ad libitum* level of food provision on which competition for food would not be expected to occur, (ii) 100 mg which is moderately limiting, and (iii) 50 mg which is severely limiting. The outcome of competition at each food level is shown in Table 4.

Table 4. *Survival to adult, and the duration of the period of development from hatching of the egg to eclosion of the adult fly, in the fast and slow feeding strains competing on different amounts of yeast*

(Each mean ± S.E. is based on ten replicate cultures at every level of food availability. Each culture initially contained 50 fast and 50 slow feeding larvae.)

	Survival (angles)		Development time (log h)	
	Slow	Fast	Slow	Fast
S*spa* *v.* F (mg)				
50	6·8 ± 3·2	14·3 ± 5·3	2·358 ± 0·009	2·339 ± 0·005
100	46·7 ± 2·5	59·0 ± 1·2	2·313 ± 0·003	2·290 ± 0·002
200	60·0 ± 1·3	65·2 ± 1·2	2·321 ± 0·001	2·297 ± 0·001
S *v.* F*spa* (mg)				
50	1·2	42·3 ± 3·4	2·398 ± 0·019	2·292 ± 0·003
100	24·7 ± 6·2	60·4 ± 2·4	2·357 ± 0·002	2·292 ± 0·004
200	61·1 ± 2·5	56·7 ± 2·6	2·351 ± 0·001	2·309 ± 0·002

At the highest level of food provision (200 mg) the F strain appears to have a small but significant advantage in survival rate to the adult stage over the marked slow strain S*spa*, whereas the alternative pair of competing strains S and F*spa* do not differ significantly. The two slow feeding stocks S and S*spa* were very closely similar in their survival rates, but the two fast feeding strains differed by 8·5 % suggesting that substitution of the *spa* marker was not entirely neutral in effect, even though it caused no significant change in mean feeding rate. As expected, slow feeding larvae take longer on average to complete their period of development than the fast feeders. The delay was 11 h (S*spa* *v.* F) and 20 h (S *v.* F*spa*), respectively, under the non-limiting conditions. At each of the limiting levels of food supply fast feeding larvae had significantly higher survival rates than slow feeders, even after allowing for the initial difference in viability between S*spa* and F at the unrestricted level of food supply. The differences in competitive ability are most clearly expressed in the 50 mg yeast cultures in which food shortage and competition would be most acute. Again we observe a difference in performance of the fast strains, F*spa* being clearly the more successful. These results confirm the prediction

that differences in feeding rate influence the outcome of competition between larvae when food resources are limiting for survival. Fast feeding larvae, by virtue of their attaining the minimum weight for pupation in advance of their competitors, ensure the completion of their development to the imaginal stage even though food resources may run out during the postcritical growth period. But the 'non-essential' utilization of resources by larvae in their post-critical phase may mean that the available food supply is then insufficient to allow the slow feeding larvae to achieve the critical weight necessary to complete their development.

Table 5. *Body weight in mg (mean* ± S.E.) *for adult flies from fast and slow feeding larvae in competition on different amounts of yeast*

	♀♀		♂♂	
	Slow	Fast	Slow	Fast
S*spa v.* F (mg)				
50	0·23 ± 0·03	0·21 ± 0·03	0·17 ± 0·04	0·20 ± 0·03
100	0·43 ± 0·02	0·50 ± 0·03	0·34 ± 0·01	0·41 ± 0·02
200	0·86 ± 0·03	0·93 ± 0·03	0·64 ± 0·03	0·74 ± 0·03
S *v.* F*spa* (mg)				
50	0·10	0·30 ± 0·02	0·05	0·26 ± 0·02
100	0·30 ± 0·02	0·48 ± 0·06	0·27 ± 0·02	0·44 ± 0·03
200	0·92 ± 0·03	1·06 ± 0·03	0·73 ± 0·02	0·77 ± 0·01

We must now direct our attention to adult body weight in Table 5. Both genotype groups show a marked decline in body size associated with dietary restriction and increased level of larval competition. Although there was no appreciable reduction in development rate, adult flies emerging from the 100 mg culture showed a significant reduction in body size in both sexes. The 50 mg cultures showed extreme reduction in body size associated with significant prolongation of the period of larval development. Indeed these cultures contained a number of some of the smallest adult flies we have ever seen. For example F*spa* flies hatching from cultures containing 50 mg of yeast had a mean body weight of only 0·28 mg (Table 5) which is considerably below the critical weight which larvae must reach in order to pupate. This is because under such very restricted conditions the available food is used up by larvae to attain the critical weight, and a considerable loss in body weight occurs due to starvation in the ensuing post-critical period. At each level of food provision fast feeding larvae gave rise to larger adults than their slow feeding competitors, except for females of the 50 mg cultures in the S*spa v.* F series where the differences in body size are not significant in either sex. The difference in body size between F and S flies is also found between pure cultures of the two genotype groups.

4. DISCUSSION

Larval feeding rate appears to be stabilized at an intermediate optimum in the sense that it responds to selection for increase or decrease from the mean level of expression of the character in an unselected population. The genetic basis under-

lying the response to selection has clearly been different in the two directions and it is worth asking why this should have been so. Part of the reason may have to do with the particular nature of the character we are dealing with. The rate of cephalopharyngeal retraction is likely to depend, for example, on various properties of the pharyngeal muscles, the rate of neural firing, and the energy supply, and so to involve the coordinate action of different physiological or neurochemical pathways. Sewell, Hunt & Burnet (1975) have detected differences in the levels of the biogenic amines noradrenalin and dopamine between the fast and slow lines. The pathways on which the character depends are separately organized and controlled, but 'tuned' overall by the action of natural selection to an optimum level of performance with respect to feeding rate. It is not difficult to visualize that impairment of any one of them could have the effect of rate limiting the system as a whole. The recessive effects of chromosomes from the slow line suggest, although they do not prove since only aggregate effects are observed, that progress in response to selection has been brought about by accumulation of recessive alleles at a number of independent gene loci, any one of which is individually capable of impairing the performance of one or other of the relevant pathways.

The conditions required to effect an increase in feeding rate over the mean of the unselected population are likely to be even more complex. A change in any one pathway potentially capable of promoting a higher rate of feeding may have no effect because other pathways controlling the expression of the character now act as limiting factors. Thus, coordinate change at several points in the system may be necessary to move the rate to a supra-optimal level. The relative importance of interchromosomal interaction in the fast line, indicative of non-allelic gene interaction seems in accord with this view.

Kearsey & Kojima (1967) have argued for more detailed investigation of the genetic architecture of characters with an intermediate optimum. Present results suggest that larval feeding rate would repay more detailed study from this point of view. The character may recommend itself in this respect because it is dynamic, so that repeated measures can be made throughout the period of larval development of a single individual. Moreover, its relationship to fitness may be readily understood.

The fact that it has not proved possible to improve the speed of larval development beyond that of the control population by increasing larval feeding rate agrees with Robertson's (1963) conclusion: that larval growth rate in the precritical period is maximized in any environment to which the population is adapted, and will be difficult or impossible to increase by selection. Presumably this is because some other variable such as the efficiency of food conversion, or the intrinsic precritical growth rate itself are limiting factors. Reduction in feeding rate was associated with a lower rate of precritical larval growth, and this is in line with the fact that selection for prolongation of the larval period is usually effective (Sang & Clayton, 1957; Clarke, Maynard Smith & Sondhi, 1961), although this is not to imply that changes in larval feeding rate were necessarily the effective cause in these instances.

Under scramble type competition, in which there is a race for the acquisition of a limited food supply, feeding rate is likely to have an important bearing on the outcome of competition between genotypes at two levels, shown in the general scheme outlined in Fig. 4.

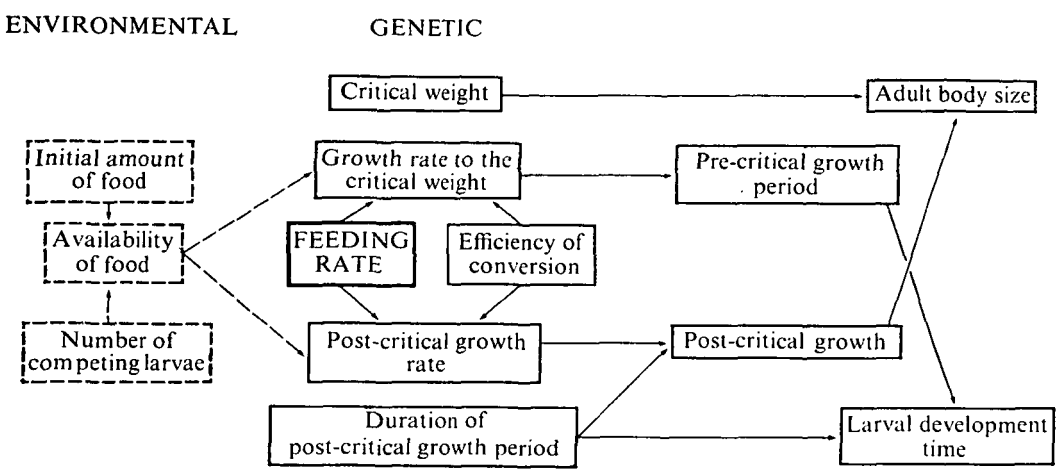

Fig. 4. A general scheme showing the relationship of larval feeding rate to other primary factors influencing growth and development.

The immediate outcome of competition between larvae in a given generation will be determined by differences in (i) feeding rate, (ii) the efficiency of food conversion, (iii) the critical weight for pupation, and (iv) growth rate during the precritical period of development. Differences between genotypes in larval feeding rate alone would be expected to determine the outcome of competition between them, other things equal, by determining which individuals reach their critical weight before the available food supply runs out. This is the first level at which larval feeding rate may influence competitive ability. The effects of differences in feeding rate are direct and conditional on the available food supply. When food supply is not limiting, larvae are able to achieve their critical weight, albeit after different periods of precritical larval growth, and so complete their development to the imaginal stage, so that there are no differences in survival rate correlated with differences in feeding rate. Our results confirm that under suboptimal conditions differences in larval feeding rate do indeed determine the outcome of competition between genotypes at this level of 'life or death' race to attain the critical weight.

Larval feeding rate may exercise an influence on competitive ability at a second level. The rate of larval feeding affects the duration of the precritical growth period and this, together with the fixed period of post-critical growth, determines larval development time. Feeding rate also influences the magnitude of the increment of post-critical growth above the critical weight, and so determines final adult body size in the imaginal insect. These effects are unconditional: they occur even when the environmental conditions for larval growth are optimal.

Large-bodied males are more successful in securing mates in a competitive mating situation (Ewing, 1961), and body size in females is phenotypically correlated with egg production (Robertson, 1957). An increase in larval development time resulting from a reduced larval feeding rate, especially if it is associated with smaller adult body size, may therefore lead to reduced reproductive success. At the second level then, the consequences of reduced larval feeding rate are indirect in the sense of being realized in the imaginal stage of the life history. Any differences in reproductive success would be expected to change the relative frequencies of larval genotypes competing in the next generation. Such prospective effects of differences in larval feeding rate beyond the generation in which it is actually measured merit more detailed investigation.

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