Directional selection in lines founded from different parts of the phenotypic distribution of sternopleural chaetae number in *Drosophila melanogaster*

D. O. F. Skibinski and N. A. K. Shereif

Biomedical and Physiological Research Group, School of Biological Sciences, University College of Swansea, Singleton Park, Swansea SA2 8PP, UK

Summary. Divergent directional selection lines were initiated from base populations founded from parents taken from different parts of the sternopleural chaetae distribution in a cage population of *Drosophila melanogaster*. Lines founded from parents taken from the central part of the distribution showed greater response and higher realised heritability than lines derived from parents with extreme high or extreme low chaetae number. The results suggest that centrally derived phenotypes have higher heterozygosity for chaetae factors than extreme phenotypes and that these factors have a large effect on the character.

Key words: Directional selection – Heterozygosity – Sternopleural chaetae number – *Drosophila melanogaster*

Introduction

In natural populations, most traits other than viability and fertility are thought to be under the influence of stabilising selection (Thompson and Thoday 1979). The theoretical consequences of stabilising selection are, however, not yet completely understood. Mather (1941) argued that stabilising selection would lead initially to an increase in frequency of genotypes made up of balanced gametes with alleles at different loci in the repulsion linkage phase. In the long run, however, stabilising selection on an additive scale should lead to fixation and loss of genetic variation (Wright 1935; Lewontin 1964; Bulmer 1980). This occurs because of selection in favour of homozygotes for balanced gametes and because in a multilocus system, selection at individual loci may be too weak to oppose drift to fixation. Lande (1983) has shown that if a segregating locus has a major effect on the character under consideration, selection in favour of intermediate heterozygotes at this locus will not easily maintain a

polymorphism in the presence of polygenic variation. Laboratory experiments on artificial stabilising selection on quantitative characters have in the main demonstrated the reduction in genetic variation predicted by theory (e.g., Thoday 1959; Prout 1962; Scharloo 1964; Gibson and Bradley 1974).

There is also evidence for balanced gametic combinations of polygenes in populations experiencing stabilising selection. For example, Thoday and Gibson (1972) extracted chromosomes from *Drosophila* males taken from stabilising selection lines and demonstrated a negative correlation between second and third chromosomes in their effects on sternopleural chaetae number. Gibson and Thoday (1962), in a study of polygenic variation underlying sternopleural chaetae number, demonstrated that 46 out of 48 second chromosomes extracted from a base population had the balanced gametic type '+ −' with respect to two chaetae loci, while the remaining two had the gametic type '− +'.

However, although studies of laboratory populations of *Drosophila melanogaster* have demonstrated the existence of strong stabilising selection for sternopleural chaetae number (e.g., Barnes 1968; Kearsey and Barnes 1970), such stabilising selection is not associated with low genetic variation; sternopleural chaetae number usually exhibits high heritability and responds well to directional selection. This can be explained in a number of ways. Lewontin (1974) has pointed out that with tight linkage the approach to fixation may be extremely slow. A "quasi-equilibrium" can be attained where heterozygotes for balanced gametic combinations are maintained at high frequency and where there is strong linkage disequilibrium. This does not occur unless there is tight linkage of the polymorphic genes affecting the character.

A number of theoretical studies indicate that the effect of stabilising selection in reducing variation may be

counteracted by recurrent mutation and result in the quite high heritability values commonly observed for quantitative characters (e.g., Latter 1960; Lande 1976; Bulmer 1980). Turelli (1984) reviewed and extended a number of models and concluded that mutation-selection balance could maintain appreciable genetic variation only if mutation rates are quite high, if the stabilising selection is neither too weak nor too strong and if the number of loci contributing to the variation is quite large. It appears that the heterozygosity of the favoured phenotypes will be negligibly higher than less fit extreme phenotypes and that there will be negligible heterozygous advantage.

Another possible explanation for high levels of variation for quantitative characters like sternopleural chaetae number is that this variation is maintained by heterozygous advantage. This could occur if there is overdominance with respect to fitness at loci which have additive pleiotropic effects on the character (Falconer 1981). The involvement of pleiotropy is supported by evidence that central sternopleural chaetae phenotypes have higher larval viability (Kearsey and Barnes 1970). In this model, central phenotypes have higher fitness and higher heterozygosity, provided that some of the genes have a large effect on the character. This higher heterozygosity could also be due in part to the greater power of developmental homoeostasis of heterozygotes (Lerner 1954). The overdominance in fitness could also account for the selective maintenance of multilocus polymorphisms. Turelli and Ginzburg (1983) have shown that when multilocus polymorphisms are maintained by selection, the fitness of individuals tends to increase with the number of loci at which they are heterozygous.

The models involving mutation-selection balance and those involving selection alone thus make somewhat different predictions about heterozygosity in relation to deviation from the mode. The former predicts that there will be little if any difference between central and extreme phenotypes, while the latter predicts a high heterozygosity for central phenotypes. Although there is evidence that central phenotypes have higher heterozygosity for allozyme loci (Beardmore and Shami 1979; Shereif and Skibinski 1988a), there is little direct evidence about genetic structure in relation to deviation from the mode or mean of characters such as sternopleural chaetae number in unselected laboratory populations.

The experiments described in this paper were designed to investigate the effect of directional selection in populations founded from central and extreme regions of the phenotypic distribution of sternopleural chaetae number in a laboratory population of Drosophila melanogaster. If central phenotypes are more heterozygous for chaetae factors than extreme phenotypes, the response to selection and realised heritability should be higher for lines founded from the central phenotypes.

The laboratory population used in the study is known to be under stabilising selection for sternopleural chaetae number and to have higher allozyme heterozygosity for central than for extreme phenotypes (Shereif and Skibinski 1988a, b).

Materials and methods

The experiments were carried out using a strain of Drosophila melanogaster called Chateau Tahbilk, which was derived from founders captured at a vineyard of the same name in Melbourne, Australia in 1979. The strain has been maintained at Swansea as a cage population at 25 °C under conditions of continual lighting. In the selection experiments, flies were raised in 25-mm diameter × 100-mm long glass vials, each containing 10 ml of a standard food medium (Mittler and Bennet 1962). Sternopleural chaetae number was scored as the sum of the macro- and micro-chaetae on the left and right sides of the fly.

One hundred single-pair crosses were set up using virgin male and female flies. Mating was assortative. From each of 97 successful matings, three male and three female progeny were scored for chaetae number. Mean chaetae number of the progeny is plotted against mid-parent value in Fig. 1. Heritability was measured to be 0.56. Twenty crosses out of the 97 were then selected to initiate 20 separate founding populations from which to begin the selection experiments. These 20 crosses are indicated in Fig. 1 and were chosen by using progeny mean as well as parental phenotype as a selection criterion. The use of both criteria rather than parental phenotype alone permits more accurate identification of genetically extreme and central parts of the chaetae distribution. Using this approach, six vials were selected from the high extreme part, six vials from the low extreme part, and eight vials from the central part of the chaetae distribution. The three males and three females scored for chaetae number for each of these 20 vials were then transferred to 20 fresh vials to become the base populations (G_0 generation) for subsequent directional selection. From the virgin progeny emerging in each of these 20 vials, ten males and ten females were scored for chaetae number. The three males and three females with the highest and the three males and three females with the lowest chaetae number were selected as parents of the next generation for an upward and downward selection line, respectively. Thus each of the 20 selected pairs gave rise to 2 lines which were selected directionally and divergently for sternopleural chaetae number. In each of the 40 selection lines, 3 males and 3 females were chosen as parents each generation out of a total of 10 progeny of each sex scored. Selection was carried out for 20 generations in all of the lines.

The lines founded from the high, low and central parts of the chaetae distribution will be referred to as high, low and central lines, respectively. Thus there were six types of line in all, high upward, high downward, low upward, low downward, central upward and central downward.

The average response to selection per generation (R) for each selection line has been estimated as the slope of the regression of progeny mean chaetae number on generation number. The selection applied per generation has been measured by the selection differential, which is the mean phenotypic value of individuals selected as parents expressed as a deviation from the generation progeny mean. The average selection differential per generation (S) has been measured for each line as the regression of accumulated selection differential on generation number. The realised heritability (h^2) was calculated for each line as the regression of generation mean on the accumulated selection differential (Falconer 1981). To facilitate comparison of upward and

Table 1. Response (R) and selection differential (S) per generation, and realised heritability (h^2) for upward and downward selection for generations G_0-G_{10} and G_0-G_{20} for high (H), low (L) and central (C) lines. Note that each of the tabulated values is the mean $\pm$ standard error of either six (H or L lines) or eight (for C lines) independent replicates

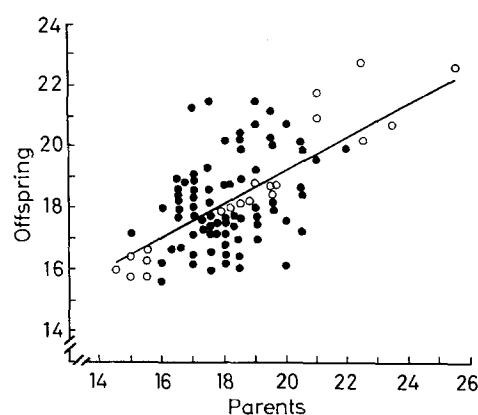|	R			S			h^2		
	H	L	C	H	L	C	H	L	C
Upward G_0-G_{10}	1.02±0.10	0.55±0.05	1.00±0.07	1.99±0.22	1.94±0.18	2.05±0.10	0.52±0.05	0.28±0.03	0.50±0.04
Downward G_0-G_{10}	0.44±0.06	0.48±0.05	0.56±0.05	1.36±0.20	1.31±0.11	1.38±0.07	0.34±0.03	0.38±0.05	0.42±0.05
Upward G_0-G_{20}	0.67±0.03	0.44±0.03	0.74±0.01	2.15±0.14	1.89±0.14	1.93±0.10	0.33±0.02	0.24±0.02	0.38±0.02
Downward G_0-G_{20}	0.33±0.03	0.29±0.02	0.39±0.01	1.34±0.11	1.01±0.06	1.20±0.06	0.25±0.01	0.27±0.02	0.31±0.02

Fig. 1. Mean sternopleural chaetae number of offspring plotted against mid-parent for single pair crosses. o – crosses selected to initiate selection lines; ● – other crosses. The regression of offspring on mid-parent is shown as a straight line
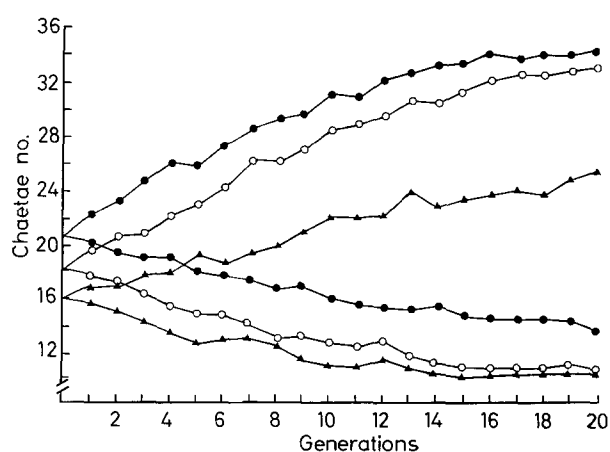

Fig. 2. Mean response (averaged over replicates) plotted against generation number for high (●——●), central (o——o) and low (▲——▲) lines

downward selection, the sign of response and selection applied in the downward direction has been changed from negative to positive.

Results

The responses averaged over replicates for each of the six types of selection line are shown in Fig. 2. For the high and central lines, at least, the response appears to have reached a plateau by the end of the experiment. Because of this non-linearity of response, the 20 generations of selection were divided into 2 periods (G_0-G_{10} and $G_{10}-G_{20}$), within which the responses were more or less linear. Values of R and S per generation and h^2 have been computed for all of the 40 selection lines for both of these periods. Values for the entire period of selection (G_0-G_{20}) have been obtained by taking the arithmetic mean of the values for the two periods G_0-G_{10} and $G_{10}-G_{20}$. The values obtained for each type of line averaged over replicates for G_0-G_{10} and G_0-G_{20} are given in Table 1. Analyses of variance were carried out on the data of Table 1, using differences between replicates as error variance. The results are given in Table 2.

First, two-way analyses were carried out to test for interactions between direction of selection and part of distribution for G_0-G_{10} and G_0-G_{20}. The total number of subgroups is thus 2 (up and down) × 3 (high, central and low) = 6. Each of the four high and low subgroups have six replicates each, the two central subgroups have eight replicates each. The total degrees of freedom are thus $(4 \times 6 + 2 \times 8) - 1 = 39$. The first two rows of Table 2 show that significant interactions occur for R and h^2. Therefore, subsequent analysis was carried out separately for the results for upward and downward selection. Table 2 also shows results of an analysis of divergent selection. The response and selection applied for divergent selection are measured from the difference between the two sister lines (one selected upwards, the other

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Table 2. Summary of analyses of variance of response of (R), selection differential (S) and realised heritability (h^2). The F values for comparison with error mean square are tabulated with significance levels

Source of variation	Degrees of freedom	R	S	h^2
Interaction–Part of distribution × Direction G_0-G_{10}	2	7.27**	<1	5.42**
Interaction–Part of distribution × Direction G_0-G_{20}	2	13.01***	<1	5.31*
Part of distribution (for Upward selection G_0-G_{10})	2	11.86***	<1	11.55***
Part of distribution (for Upward selection G_0-G_{20})	2	45.16***	1.19	13.55***
Part of distribution (for Downward selection G_0-G_{10})	2	1.14	<1	<1
Part of distribution (for Downward selection G_0-G_{20})	2	6.39**	4.22*	3.21
Direction (G_0-G_{10})	1	46.00***	28.80***	2.67
Direction (G_0-G_{20})	1	257.44***	89.65***	7.42**
Part of distribution (Divergence G_0-G_{10})	2	5.97*	<1	4.47*
Part of distribution (Divergence G_0-G_{20})	2	32.30***	5.94*	22.88***

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Table 3. Differences in response (R), selection differential (S) and realised heritability (h^2) between high (H), low (L) and central (C) lines

			Differences between lines		
			(H–L)	(H–C)	(C–L)
G_0-G_{10}	Upward	R	0.47**	0.02	0.45**
		S	0.05	−0.06	0.11
		h^2	0.24**	0.02	0.22**
G_0-G_{10}	Downward	R	−0.04	−0.12	0.08
		S	0.05	−0.02	0.07
		h^2	−0.04	−0.08	0.04
G_0-G_{20}	Upward	R	0.23**	−0.07	0.30**
		S	0.26	0.22	0.04
		h^2	0.09*	−0.05	0.14**
G_0-G_{20}	Downward	R	0.04	−0.06	0.10**
		S	0.33*	0.14	0.19
		h^2	−0.02	−0.06	0.04
G_0-G_{10}	Divergence (Up–Down)	R	0.43†	−0.10	0.53*
		S	0.11	−0.07	0.18
		h^2	0.10	−0.03	0.13*
G_0-G_{20}	Divergence (Up–Down)	R	0.26**	−0.14*	0.40**
		S	0.60**	0.36	0.24
		h^2	0.04*	−0.06**	0.10**

† $P=0.05$
* $P<0.05$
** $P<0.01$

downwards) from each of the 20 single pair crosses chosen initially. The values for divergent response (R) will reflect the amount of divergence between the upward and downward lines of a given part of the distribution. Differences in R, S and h^2 between the high, low and central lines have been calculated for upward and downward

selection (from the means in Table 1) and for divergent selection, and are given in Table 3. Where the mean square for part of distribution was significant (Table 2), the three possible comparisons between mean values (high versus low, high versus central and central versus low) were made using the GT2 and T′ methods as described in Sokal and Rholf (1981). Significance levels obtained in this way are attached to the mean differences given in Table 3. The values of R for G_0-G_{20} are less than those for G_0-G_{10} as a result of the asymptotic nature of the selection response.

On the whole, R is greater in the upward than downward selection lines (Tables 1 and 2). There is, however, a significant interaction between part of distribution and direction (Table 2). This appears to be the result of a difference in response of the low versus high and central lines. Thus for upward selection, R is significantly greater for the high and central than the low lines, while with downward selection the responses of all types of lines are much more similar (Tables 1 and 3). R is, however, consistently greater (with one exception) in the central than high and low lines (Table 1), though significant results are obtained only in comparisons between central and low lines. In both directions of selection, a high percentage of the variation in response is attributable to the differences between parts of the distribution (Table 2). The contrast between the three types of line is magnified in the divergent response (Table 3). For G_0-G_{20}, R is significantly greater for the central than high lines.

The differences in pattern of response may be readily appreciated from Fig. 2. For example it is easy to see that the magnitude of the divergent response occurs in the order central > high > low lines.

The values of R given in Table 1 do not provide sufficient information to deduce the mean chaetae values attained at the end of the experiment. This is because the starting points at G_0 differ between the lines derived from the different parts of the distribution (Fig. 2). For example, the downward responses of the high and low lines are closely similar (Tables 1 and 3), but because selection in the low lines was initiated at a lower chaetae number, the selection limit attained is lower than in the high lines. Similarly, although the central lines show the greatest divergent response, the upper and lower selection limits do not exceed those attained in the high and low lines respectively.

Unlike R, the selection applied (S) shows no significant interaction between part of distribution and direction of selection (Table 1). However S, like R, has significantly higher values in the upward than downward direction (Tables 1 and 2). The low lines have consistently lower mean values of S (Table 1), though the differences between parts of the distribution are small and non-significant, except for the comparison between high and low lines which is significant for both downward and divergent selection for G_0-G_{20}.

Realised heritability (h^2) is a function of, and will thus not be expected to vary independently of, response and selection differential. For example, both R and S are greater in the upward than downward selection lines. Because h^2 is related to the ratio R/S, h^2 may be expected to show less difference between upward and downward selection than either R or S. This is what is observed; the percentage of the variance in h^2 attributable to direction of selection is relatively small (Table 2). Also, because S shows much smaller differences between parts of the distribution than R does, the pattern of variation in h^2 and R should be closely similar. This is what is observed; large or significant values for R are usually matched by large or significant values for h^2 (Tables 2 and 3). For example, for G_0-G_{10}, R and h^2 both show large and highly significant variation between parts of the distribution in the upward direction, while the variation in S is small (Tables 2 and 3). By contrast, in the downward direction both R and h^2 show little variation, as does S. This pattern of variation in R, S and h^2 can also be seen clearly in Table 1.

Discussion

The experiments described in this paper were designed to compare the effectiveness of directional selection for sternopleural chaetae number in selection lines founded from different parts of the normal phenotypic distribution of the character. The results provide evidence that lines founded from central phenotypes show greater response to divergent selection than lines founded from

high or low extreme phenotypes. This greater response of the central lines is not the result of a higher applied selection differential but is associated with a higher realised heritability. It may thus be concluded that the cause of the greater response is the existence of greater genetic variation, and presumably higher heterozygosity and intermediate gene frequencies for chaetae factors underlying central rather than extreme phenotypes. The results are, therefore, less in agreement with the model of mutation-selection than with that involving overdominance with respect to fitness of factors having a relatively large effect on the character.

The observed responses appear in other ways to favour a model of a small number of genes with large effect. Such a model predicts, first, that the response to selection will be exhausted rapidly (Robertson 1960). This is observed here. Second, it predicts that replicate lines will converge as they approach the selection limit, rather than showing the increasing divergence expected as a result of genetic drift on a character controlled by many loci. Table 4 shows the phenotypic variance of replicated line means at G_{10} and G_{20}. In most instances the variance at G_{20} is smaller than at G_{10}, which is consistent with convergence towards a limit. Some differentiation between replicates lines is, of course, expected as a result of sampling effects or recombination even under a model with a small number of genes (Hollingdale 1971).

Asymmetry of response between upward and downward directional selection as observed in these experiments is a common feature of selection experiments in *Drosophila* (e.g., Mather and Harrison 1949; Clayton et al. 1957; Robertson 1977; Serra and Oller 1984) and has several possible causes (Falconer 1981). Additional complications in relation to asymmetrical response occur in the present experiments. First, the downward selection lines initiated from high extreme phenotypes and the upward selection lines initiated from the low extreme phenotypes responded relatively poorly, and second, the former showed a greater response than the latter. The

Table 4. Phenotypic variance of mean sternopleural chaetae number between replicate selection lines in G_{10} and G_{20}

Type of line	Variance (G_{10})	Variance (G_{20})	F
High (upward)	8.76	0.09	101.06**
High (downward)	1.01	4.64	4.59
Low (upward)	1.70	2.25	1.32
Low (downward)	0.73	0.19	3.78
Central (upward)	2.75	1.20	2.46
Central (downward)	3.54	0.10	36.77**
All lines (between replicates within type of line)	3.09	1.30	2.37*

* $P<0.01$
** $P<0.001$

first effect may be attributed to the preferential loss of high and low chaetae factors during the initial founding event or early stages of selection. High chaetae factors would, for example, be lost more readily by sampling effects in the low lines because they would initially be at a relatively low frequency. The second effect may be explained if it is assumed that gene frequencies are initially at more extreme values in the low than in the high lines. Dominance of high over low chaetae factors, for which there is some direct evidence for this character (e.g., Skibinski and Thoday 1979), may be partly responsible for such an asymmetry of gene frequencies between high and low lines.

The final gain in response at the selection limit is expected to depend on effective population size as well as on selection differential and realised heritability (Robertson 1960). The present results demonstrate, in addition, that founder effects may markedly affect the response to selection.

Unfortunately these results do not suggest any practical advantage for initiating lines from central phenotypes. Although the lines derived from central phenotypes showed greatest response and realised heritability they did not, because of their central starting point, attain the most extreme limits to selection in either direction. These lines would have had, at the beginning of the selection experiment, higher frequencies of multiple heterozygous genotypes than the base population or the other selection lines. This might have increased the probability of the breakage, through recombination, of unfavourable linkages in repulsion heterozygotes present in the base population. Such events, associated with accelerated responses to selection (e.g., Thoday et al. 1964), would however not have been facilitated by the small effective population size, which instead would lead to rapid fixation.

A number of studies have been made of patterns of directional selection which involve a departure from the conventional system of selecting, within a single population, the most phenotypically extreme individuals as parents each generation. For example, experimental comparisons of selection in subdivided and undivided populations have been made in several organisms (e.g., Bowman and Falconer 1960; Goodwill 1974; Katz and Young 1975; Madalena and Robertson 1975; Rathie and Nicholas 1980). The expectation of a greater response in the subdivided populations (e.g., Wright 1978) was realised only in the experiment of Katz and Young (1975). Studies have also been made on the relationship between selection intensity and response in *D. melanogaster* (Clayton et al. 1957; Frankham et al. 1968; Yousif and Skibinski 1982). In most instances these experiments, in common with those described in this paper, involved the selection as parents of some individuals with more centrally located phenotypes. They also demonstrated that lower selection intensities result in higher realised heritability but no overall advantage with respect to gain when selection is terminated.

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