REVERSAL OF A SECONDARY SEX CHARACTER
BY SELECTION

B. J. HARRISON

John Innes Horticultural Institution, Hertford

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I. INTRODUCTION

PAST selection work on quantitative characters, notably using *Drosophila*, has usually been made with equal rigour on both sexes. In the present account numerous lines, from the same F_2 , have been differentially selected with respect to the sexes within the same line. Since the effective response to selection depends upon the correspondence between genotype and phenotype, any sexual difference in the correlation between genotype and phenotype would result in selection acting with different speeds in the two sexes.

The failure of the phenotype to mirror exactly the genotype in all individuals from a culture means that in many selections individuals are selected which are genetically lower or higher than expected. If a mid level is required, this inaccuracy becomes more apparent than if high or low selections are being considered. In the case of extreme selections the direction is definite and any inaccurate selections will not affect the next generation so markedly, for the top or bottom stratum of the population is already represented in the selected individuals. In a mid selection there may be slight inaccuracies in selection. For example the environment may affect one or other level preponderantly and thus offer for selection individuals which are mostly from one extreme of the population and will result in a gradual drift of the mean. This implies directional interaction of genotype and environment. In general, mid-lines may be expected to drift more than the extremes but to drift erratically without specific and continued direction. In the selections under review the best methods for mid level continuation are demonstrated.

The fertility of selected lines is usually impaired by continued successful selection. Selection for particular genotypes will undoubtedly disturb the normal good fertility to some extent by correlated response but as most selections also tend to inbreed the population these two factors must act concurrently. The difference in rigour among the twelve selections gives an opportunity to study the effects on fertility of selection, for inbreeding was constant in all twelve lines.

2. EXPERIMENTAL METHOD

Selection was practised on the abdominal chaetæ of *Drosophila melanogaster* described by Mather, 1941. Two inbred lines, Oregon+ (inbred for 250 generations) and Samarkand+ (inbred for 150 generations) were crossed reciprocally and a large F_2 was made up from the two reciprocal F_1 's. The variously selected lines were taken from the F_2 . The selections, apart from the F_2 when 80 flies of each sex were counted, were made on counts of 20 ♀♀ and 20 ♂♂. Two cultures, one a reserve, were made from each line using 2 ♀♀ and 2 ♂♂. The reserve was never used unless the principal culture failed, which was seldom. Variability, therefore, was not preserved to the same extent as in the method employed by Mather and Harrison (1949) and the response cannot, in consequence, be expected to be so great.

The whole experiment was repeated later using the same inbred material and using the same technique in order to assess more accurately the effects of the different selective methods. So much seems to depend on the accuracy of genotype selection in the first few generations that for a proper assessment of the responses several replicates would have been preferred but, due to the prodigious labour this would have involved, only two were done.

The twelve selected lines are listed below together with their symbols which will be used throughout this account :—

♀♀ selected	♂♂ selected	Symbol
High	High	HH
High	Mid *	HM
High	Low	HL
Mid	High	MH
Mid	Mid	MM
Mid	Low	ML
Low	High	LH
Low	Mid	LM
Low	Low	LL
Mid	Alternating High and Low †	M (H and L)
Alternating High and Low	Mid	(H and L) M
Alternating High and Low	Alternating High and Low	(H and L) (H and L)

* The mid selection is at the mean of the particular sex in the culture counted at that generation.

† Selection alternates each generation, *i.e.* first generation of selection was high, second low, third high, etc. ♂♂ and ♀♀ both alternated in the same direction at the same time.

3. CULTURE VARIATION

It has already been pointed out that inaccuracies in selection are likely to occur in a highly variable culture. This is due to developmental differences within a culture which affect the expression of chaeta number to some extent. A comparison of the variances of a group of F_2 means with the mean of the same F_2 variances shows, however, that the difference between cultures is relatively low, while the variation within a culture is, as expected, much higher. This shows that the variation due to unknown environmental causes is

due in the main to variation between individuals in a culture and not to variation between the cultures. A little variation between cultures does occur, as demonstrated by Mather, 1949.

TABLE 1

Mean chaeta number of 11 F ₂ 's (Or. $\times$ Skd) (20 ♂♂ counted in each class)		Mean squares on corresponding groups of the 20 ♂♂	
1. 34.55	Mean square 0.268	4.137	Average mean square 5.945
2. 34.75		6.421	
3. 34.95		2.158	
4. 34.85		5.421	
5. 34.5		4.158	
6. 35.1		4.158	
7. 33.35		8.947	
8. 33.55		12.263	
9. 33.7		6.316	
10. 34.7		4.211	
11. 34.55		7.211	

Temperature and culture condition do not affect the expression of chaeta number very greatly but the unknown developmental differences can give considerable differences in the variances. Culture 3 has a low variance of 2.158, but culture 8 gives an estimate of 12.263. The selective sieve will doubtless vary in its efficiency if the individuals within the cultures can vary so greatly. It is the development of the individuals within a culture that is, in some cases, masking genetic differences between individuals. Between lines, which is the comparison in which we are interested, the quirks of development may be expected to cancel each other out and the comparison of culture means is therefore a reliable appraisal of the genetic conditions prevailing in the line.

4. SELECTION LINES

The complete data from the twelve selected lines together with the repeat experiment are presented in the accompanying graphs (figs. 1 to 4). These show the comparison of the duplicated selections.

HH. The response in HH1 (the first experiment) was the same until S7 (the seventh generation of selection) as in the line in the second experiment, hereinafter called HH2. But HH1 rose slowly after S7 while HH2 failed to respond at all after S7.

HM. These two lines responded very differently. HM1 fell slightly until S12 and then stabilised itself, while HM2 rose steadily for the whole 17 generations. This comparison is an object lesson in the way in which two similarly selected lines follow different paths. This difference in response may be due either to the different genetic potentialities of the first parents chosen or to the difference in the genetic make-up of the mid males, which being most heterozygous, are perhaps most likely to vary in response according to the vagaries of recombination while

some might fail to respond owing to chance homozygosity for recombinations of mid effect. One other possibility may be mentioned, namely that chromosomal selection of one or other set of inbred chromosomes might have been selected before recombination took place in HM1 thus minimising the polygenic variability available

FIGS. 1-4.—The response of the various selections. Solid lines show the means of the sexes; dotted lines the females and broken lines the males.

for release. The reciprocal selection, MH, also responded differently in the two experiments while all other lines were on the whole similar.

HL. HL1 fell a little until S3 and stabilised itself for the remaining 14 generations. HL2 on the other hand rose a little and then fell slightly. In these two opposed selections the pull between selected ♂♂ and ♀♀ was about equal for apart from the first and perhaps the last few generations the lines did not respond.

MH. It was mentioned in the reciprocal selection, HM, that the divergence of the two experiments is perhaps greatest in this type of selection. Whether this divergence is consequent upon the type of selection or merely fortuitous is unproved. MH1 rose steadily until S₉ and from there remained fairly stable. MH2, however, remained stable throughout the seventeen generations of selection.

MM. MM1 died at S₄ and had to be remade from M (H and L) ♀♀ and

FIG. 2.

(H and L) M ♂♂ obtained from S₆ cultures. These two lines were thought to approximate as near as possible to the MM selection. The mean of MM2 and the repeat of MM1 drift down steadily though slowly for the run of the experiment. It would seem that for a stable mid line the MM type of selection is not the most satisfactory.

ML. ML1 responded in a low direction throughout the selection. Here the power of the low selection on the ♂♂ as compared with the mid selection on the ♀♀ cannot be effectively established as ML2 died prematurely at S₆. However,

it appears from the other lines in which a mid selection was used that whenever the other sex was selected in any way other than in a high direction the line never responded in a + direction. The mid selection, therefore, would seem incapable of giving a high boost to the selection.

LH. In this opposed selection there is closer agreement between the replicates than in the reciprocal selection, HL. There is very little departure from the point

FIG. 3.

of commencement and it seems that the low female selection and the high male selection have balanced each other. No greater release or build-up of high or low polygenic complexes has therefore been favoured in this set.

LM. The LM lines both responded in a low direction and were equal in response to the LL selected lines. LM1 and LM2 both showed a curious reversal in the number of chaetæ produced by ♂♂ and ♀♀. This phenomenon will be dealt with in greater detail later in the account.

LL. Both lines responded similarly, LL2 responding a little more than LL1. No increased response in a low direction occurred after S11 when both lines become stable. The low level reached by the LL lines was no more than that reached by many other selections under discussion.

M (H and L). These two lines responded in a similar fashion to the LL lines except that no more response occurred after S₇. Here it is evident that in this material a low response is easier to obtain than a high.

(H and L) M. The first line of this selection remained at the mid level throughout the seventeen generations of selection with some fluctuations. (H and L) M₂ remained at a slightly lower level, except for a rise at S₆ and S₁₇.

FIG. 4.

(H and L) (H and L). The first line remained about the mid level throughout while (H and L) (H and L)₂ was a little higher towards the end of experiment following a rise at S₉.

If we summarise the results of these various selections further we have those which responded and those which remained unchanged in both experiments, in the first experiment only and in the second experiment only.

Although it is possible to hazard some conclusions from table 2 it must be emphasised that they rest on two sets of data only. The overall responses are small and this is unfortunate for it does not allow an accurate assessment of line differences. If we consider the selections in the first experiment then we could say that the ♂♂ are

TABLE 2

	In expt. 1 and 2	In expt. 1 only	In expt. 2 only
Good response High	...	MH HH	HM
Slight response High	...	...	HH (H and L) (H and L)
Good response Low	LM, M (H and L) LL	ML	...
Slight response Low	MM	HM, HL	...
Mid level	LM, (H and L) M, LH	(H and L) (H and L)	HL, MH

less efficient in the production of a high chaeta number under selection but if we pool the data from the two experiments, as we must, then this sexual difference in the response to selection disappears.

If the sexes do not differ in their ability to respond to selection which seems to be the case from these data, then in an opposed selection like LH or HL the relative ability to release plus or minus variability must be shown by the direction of response. Neither LH nor HL (in both experiments) can be said to show any striking response in either direction. The double alternating selection (H and L) (H and L) also remains near or at the mid level. These results indicate that in this material no more release of variability is found in one direction over the other and show that selection is equally effective in both sexes.

5. FERTILITY OF THE LINES

Fertility counts were made on all the lines in the first experiment. This was measured by taking the total number of flies emerging from the culture. The figures listed below are averages of flies per bottle of the lines over the whole seventeen generations.

LL 280	ML 230
HH 255	(H and L) M 210
M (H and L) 230	MH 190
LH 230	HM 180
LM 230	HL 175
(H and L) (H and L) . 230	(MM not comparable due to line being remade so omitted)

The fertility of all the lines was good in both experiments and from the fertility figures obtained from expt. 1 it appears that the extremes of selection (*i.e.* HH and LL) are not deleteriously affected by selection any more than any of the other lines, in fact they head the list for good fertility. Any selection, therefore, is just as likely to upset the fertility balance as an extreme type of selection. The inbreeding of a selected stock may therefore have a considerable effect on the fertility apart from the fertility unbalance due to selection.

A comparison of the present chaeta responses with those of Mather and Harrison (1949) shows the present ones to be much lower even though the original cross was the same. As the responses were small it may be that there was not such a great correlated effect on fertility. This difference in response between the two experiments may indicate a change in the genetic make-up of Samarkand and/or Oregon inbred since its use by Mather and Harrison some eleven years earlier.

6. SEX DIFFERENCES IN CHAETA NUMBER

Normally the females have more abdominal chaetæ on the ventral surfaces of 4th and 5th segments than the males. The sex difference in chaeta number varies according to the total number of chaeta. Fig. 5 illustrates this effect. The data used for fig. 5 are obtained from the many levels obtained in the selections of Mather and Harrison (1949), which originated from the same material that was again used in this experiment, namely Samarkand $\times$ Oregon. The levels of Mather and Harrison were all established by a LL or an HH type of selection.

The relationship of sex difference to total chaeta number gives us a yard stick by which we can measure any aberrant difference. In fig. 6 we insert the regression line and limits obtained in fig. 5 and superimpose the sex differences occurring in the selection lines under discussion. Many points lie outside the limits of fig. 5 which may be due to the small effects operating on the sexes consequent upon the various selection methods. The path of regression employed is too steep or too high in overall position for the present data, for the HH lines of the present experiment fall below lowest values in fig. 5 though the sex mean is well within range. However, it appears that the spread of the variously selected lines is much greater than expected from previous experience and that the LM lines are extremely aberrant.

Sex difference has already been shown to vary with slight genetic alterations (Harrison and Mather, 1950), but never to the extent of that shown by the LM lines (fig. 3). The LM selections show a complete reversal, the females carrying fewer chaetæ than the males. This reversal, however, is due not to equal changes in both sexes but only to the females which carry fewer than normally. The males remained constant throughout both experiments. In LM1 when the

females became lower than the males at S7 the emergence of the females became about one half that of the males. In LM2 the emergence of the males and females was equal. Blackened larvæ and pupæ present in LM1 cultures were presumably the females which had failed to emerge.

If in the LM1 line crossing over had occurred between the X and Y chromosomes (Mather, 1944 ; Philip, 1935) then the females homozygous for the recombinant chromosomes may have been lethal while the heterozygous recombinant females showed the reduction

FIG. 5.—The relation between high and low chaeta number and the sex difference. (Data obtained from "Manifold Effect and Selection," K. Mather and B. J. Harrison, 1949.)

in chaeta number. The Y chromosome has been shown to be slightly active but due to its comparative inertness the recombinant would be expected to be less active polygenically than the normal X. The low female selection in these LM lines would favour the new recombinant X chromosomes while the hemizygous males with a recombinant X were not so markedly affected, the mid selection on the males not being strong enough to pick out recombinant Y chromosomes. That the phenomenon occurred again in the LM2 line may be said to be possibly fortuitous for the type of selection favouring recombinant females existed in the LH lines but, no sex differences of the LM type occurred in LH1 but in LH2, towards the end of the experiment the sex reversal began to appear. In LH2,

however, the reversal was due to the males increasing in chaeta number while the females remained at the same level. It appears to be a possibility then that the LH2 selection was favouring recombinant Y chromosomes while the selection had failed to pick out low chaeta producing recombinant X chromosomes. Had this occurred the sex reversal would doubtless have been considerable.

One other explanation for the alternation of the sex differences remains to be mentioned. It is possible that due to the sexually opposed selections practised here genes have been selected which

FIG. 6.—The sex differences obtained from the present selection lines plotted on the path of regression obtained in Fig. 5. Letters and plus sign indicate results from Experiment 1 while plain key letters indicate Experiment 2. The positions are obtained by pooling results of the last five generations of selection (*i.e.* S 13–S 17).

manifest themselves differently in the two sexes. The fact that they did not show themselves in all selections favouring such a situation must similarly be attributed to inaccuracies of selection. The poor emergence of females in LM1 may be due in this case to a correlation of chaeta genes, sex limited in expression, and genes for poor viability. Where the correlation did not exist, or was not so complete, females emerged and exhibited the sex reversal in chaeta number.

The sex differences vary materially between many of the lines. In (H and L) (H and L)₁ the difference is large throughout the experiment, while in (H and L) (H and L)₂ the difference diminishes after S8. HL₁ also shows a large difference while the rest of the lines, apart from the LMs are either less constant or the difference

is small. It is apparent that sex differences can be altered by selection but the mechanism by which they are obtained can only be conjectured here.

The similarity of response of means in reciprocal selections shows that selection is equally effective in both sexes. The changes in sex differences, however, show that it is possible to get sex-limited responses to selection. This is presumably a way sexual selection in nature produces changes in secondary sex characters.

7. SUMMARY

1. Twelve different methods of selection have been tried on the abdominal chaetæ in *Drosophila melanogaster*. The sexes were subjected to opposed, and to partially opposed, selections, e.g. ♀♀ low and ♂♂ high; ♀♀ mid level and ♂♂ high.

2. Opposed selections on the two sexes resulted in little or no response to selection. The best method for a mid level continuation of a stock is considered.

3. The fertilities of the lines tested did not indicate a greater decrease in fertility with a more rigorous method of selection owing perhaps to the total smallness of the responses.

4. The difference in behaviour of the duplicated selections shows the caution needed in interpreting the results of an isolated selection when comparisons of treatments are being made.

5. Sex differences in chaeta number vary considerably between lines and in some cases seem to be correlated with the type of selection. The relation of sex differences in chaeta number and the mean chaeta number of the sexes is disturbed by the different methods of selection when compared with an arbitrary standard.

6. Normally, ♀♀ have more abdominal chaetæ than the ♂♂, but in two selections the difference has actually been reversed. Thus a sex reversal in a secondary sex character has been obtained by selection. These reversals can equally well be explained by assuming crossing-over between the X and Y chromosomes, or selection for sex-limited genes.

8. REFERENCES

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