Genet. Res., Camb. (1990), **56**, *pp.* 57–70 *With 5 text-figures Printed in Great Britain*

Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance

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(*Received 23 January 1990 and in revised form 23 March 1990*)

Summary

To simplify the description of selection in two environments the terms 'antagonistic' and 'synergistic' are used. Selection upwards in a bad environment or downwards in a good environment is antagonistic, the selection and the environment acting in opposite directions on the character. Synergistic selection is the reverse, upwards in a good environment or downwards in a bad, selection and environment acting in the same direction. Published experiments are reviewed to see how well they agree with two expectations. First, Jinks & Connolly (1973) showed that antagonistic selection reduces environmental sensitivity and synergistic selection increases it. The experiments reviewed showed many exceptions to this rule, but they all showed that sensitivity was less after antagonistic than after synergistic selection. This is shown to be simply the consequence of correlated responses being less than direct responses. Second, I suggested (Falconer, 1989) that antagonistic selection might be the best way to improve the mean performance in the two environments. In the experiments reviewed, antagonistic selection was significantly better than synergistic for changing the mean, but it is now shown that there is no theoretical justification for this expectation; if one type of selection is better in one direction the other ought to be better in the other direction.

Expressions are given for the changes of mean performance and of sensitivity resulting from selection in one or other environment; these changes can be predicted from the parameters of the base population. In the experiments reviewed, an increase of mean performance accounted for 49% or more of the upward response. Equations are presented which allow the variance of mean performance, the variance of sensitivity, and the covariance of mean with sensitivity to be derived from parameters estimated in an unselected population, namely the variances in the two environments and the corresponding covariance. The variance of sensitivity that might be ascribed to scale effects is deduced. Directional selection in a single macro-environment is synergistic with respect to the micro-environmental differences, and is expected to increase environmental sensitivity and consequently to increase environmental variance. Stabilizing selection is antagonistic selection in both directions at the same time, and so is expected to decrease environmental variance.

1. Introduction

When a character is measured in two environments, such as growth rate on different levels of nutrition, the measurements must be treated in a genetic context as two different characters. The physiology will be different and the performance in the two environments will be influenced to some extent by different genes, though partly also by the same genes. The two characters are genetically correlated and the magnitude of the correlation reflects the extent to which the same genes are involved. A genetic correlation of less than +1 shows itself in an analysis of variance as genotype × environment interaction. If a breeder wants to improve performance in environment A he should select in environment A. This is because, if selection is made in environment B, the improvement of performance in A is a correlated response, and correlated responses are in general less than direct responses. This principle has been recognized for a long time and has been substantiated by many experiments; it does not need any further discussion here.

Animal and plant breeders, however, may want to improve the overall performance in a range of environments; or if there are just two environments,

the mean of the performances in the two environments. It is not immediately clear how this is best achieved. James (1961) studied the problem and derived formulae which show how the mean performance will be improved by selection in one or other of the two environments.

The difference between the measurements of a genotype or of a population in the two environments is the environmental sensitivity, or the reaction norm. Jinks & Connolly (1973) showed that sensitivity is reduced by selection upwards in a bad environment and by selection downwards in a good environment. This rule was restated with additional evidence by Jinks & Pooni (1988). I will call it the Jinks–Connolly rule. Generalizing from the results of experiments with mice, I suggested (Falconer, 1989, p. 325) that to increase the mean performance selection should be made upwards in a bad environment and conversely to decrease mean performance downward selection should be made in a good environment. I will show here, however, that there is no theoretical justification for this prediction, though experiments show it to be more often right than wrong.

The first object of this paper is to review the results of published experiments to see how far they conform with the Jinks–Connolly rule and what they tell us about the best way to improve the mean performance. The second object is to present some theory showing how the parameters of the sensitivity and the mean are related to the parameters that can be directly estimated in an unselected population. This theory will allow us to answer some interesting questions, such as how much of the observed variation is due to variance of sensitivity; and how much the mean and the sensitivity respond to selection for performance in one or other environment.

2. Nature of the data

(i) *Sensitivities of genotypes*

Let us first look at some experimental data to see what the problems are. Fig. 1 depicts the performance of 10 genotypes of *Nicotiana rustica*. The data are in tables 42 and 44 of Mather & Jinks (1982). The genotypes were those of 10 inbred lines, each represented by 8 individual plants. The character is final plant height. There were 8 environments consisting of combinations of 4 sowing dates and 2 planting densities.

To quantify the sensitivity we have to assign values to the environments. This is done by giving each environment a value equal to the mean plant height of all the genotypes in that environment. The sensitivity of a genotype is then the slope of the regression line of its height on the environmental value. Fig. 1 shows these linear regressions for each of the 10 genotypes and their intercepts on the two most extreme environments. Only these 2 extreme environments will be considered further though the values of the other 6 are marked by arrows on the graph.

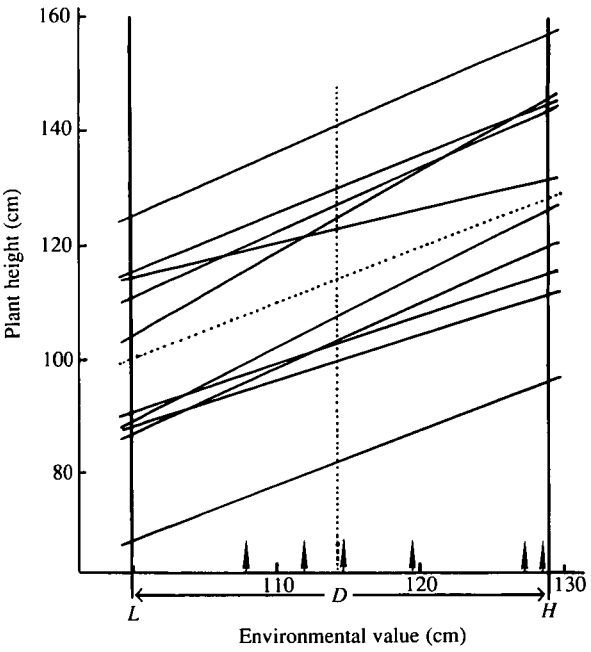

Fig. 1. Final plant heights of 10 genotypes (inbred lines) of *Nicotiana rustica* grown in different environments. The dotted lines are means. Further details in text. Data from Mather & Jinks (1982).

Three consequences follow from expressing sensitivity in this way. First, sensitivity is a dimensionless number, which facilitates comparisons between experiments; second, the mean sensitivity is necessarily equal to 1·0; and third, the regression expressing the mean sensitivity is necessarily linear. There can be objections to this method of evaluating environments that differ in more than one way, as here in sowing date and planting density. But these objections do not apply when there are only two environments, because the evaluation does no more than replace a physical measurement, such as a temperature difference, by a difference in the character measured, for example the number of eggs laid by *Tribolium*. This paper deals with only 2 environments so I shall not consider the objections further.

To apply the terms 'good' and 'bad' to the environments is confusing because what is good for increasing the character is bad for decreasing it. So I shall call the environments high (H) and low (L) according to whether they give the character a higher or a lower mean value. The difference between the values of H and L will be symbolized by D. These environments should really be called macro-environments. Within each macro-environment there are of course differences of micro-environment, but the variance due to micro-environment does not concern us except in so far as it determines the heritability in each macro-environment.

(ii) *Selection responses*

Fig. 2 illustrates the consequences of selection. It refers to the growth of mice when fed a normal diet (the high environment) and a reduced-protein diet

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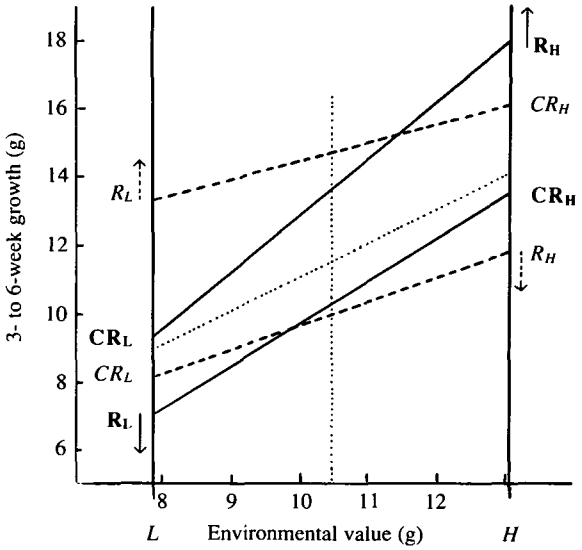

Fig. 2. Growth of mice after 5 generations of 2-way selection on different diets. The arrows show the direction of selection. Broken lines and arrows refer to antagonistic selection, solid lines and arrows to synergistic selection. The sloping dotted line is the unselected control; the vertical dotted line marks the mean performance in the two environments. Direct responses (R) and correlated responses (CR) are marked alongside the selection lines to which they refer, with the responses to synergistic selection in bold type. Subscripts to R indicate the environment of selection; subscripts to CR indicate the environment of assessment. Data from Nielsen & Andersen (1987).

(the low environment), as described by Nielsen & Andersen (1987). The low-protein diet reduced growth by 16%. The figure shows the means of 3 replicates after 5 generations of two-way selection. The sensitivities depicted are now not those of individual genotypes; they are the mean sensitivities of the populations after selection. There are four selected populations: selected up and down in the two environments, and there is also an unselected control.

Description of the selection becomes very confusing when there are two directions of selection, two environments of selection, and two environments of assessment. To remove some of this confusion I shall use the terms *antagonistic* and *synergistic* selection. When selection and environment change the character in opposite directions this is antagonistic selection, i.e. selection upwards in a low environment or downwards in a high environment. Synergistic selection is the reverse: upwards in a high environment or downwards in a low environment, when selection and environment change the character in the same direction. [The term 'antagonistic selection' has been used before, by Rutledge, Eisen & Legates (1973), in connection with simultaneous selection on two correlated characters. I hope its use here in connection with the environment will not be confusing.] Antagonistic selection is shown in Fig. 2 by broken lines and arrows, synergistic selection by solid lines and arrows. The unselected control is shown by the sloping dotted line. Representing the base population, it has a sensitivity of 1·0, as explained earlier. The mean performance in the two environments is indicated by the vertical dotted line.

The direct responses (R) and the correlated responses (CR) are marked in the figure, the responses to synergistic selection being in bold type. The realized genetic correlation, r_A, calculated by equation (19·7) of Falconer (1989) is 0·25 from the upward selection and 0·29 from the downward selection. It can readily be seen from the figure that if, in each environment, the direct response is greater than the correlated response, which it nearly always is, then the sensitivity must be less after antagonistic selection than after synergistic selection. In this experiment the sensitivity was decreased by antagonistic selection and increased by synergistic selection, both upwards and downwards. This is in accordance with the Jinks–Connolly rule. The mean performance was both increased and decreased more by antagonistic than by synergistic selection. Two similar experiments with mice (Falconer & Latyszewski, 1952; Falconer, 1960) both gave results that are barely distinguishable from those in Fig. 2.

3. Review of experiments

There are seven published experiments, some with replicates, from which we can compare the effects of antagonistic and synergistic selection on the sensitivity and on the mean performance. The references and brief descriptions of the data are given in Table 1 and the results are given in Table 2. The values in Table 2 were obtained as follows. The sensitivity of any selected line is the difference between its performances in the high and low environments divided by the same difference, D, in the base population or in a contemporaneous unselected control. The initial sensitivity is by definition 1·0 as explained earlier, so if the final sensitivity is under 1·0 selection has decreased it and if it is over 1·0 selection has increased it. The mean performance of a selected line is the mean of its performances in the high and low environments. The relative merits of the two types of selection in changing the mean is expressed as the ratio

$$\left(\begin{matrix}\text{change of mean by}\\ \text{antagonistic selection}\end{matrix}\right)\Big/\left(\begin{matrix}\text{change of mean by}\\ \text{synergistic selection}\end{matrix}\right).$$

A ratio of over 1·0 means that antagonistic selection was better, and a ratio of under 1·0 means that synergistic selection was better.

Many difficulties were encountered in obtaining the necessary data. For example, sometimes values were not tabulated and had to be read from graphs; sometimes it was difficult to decide whether to use the values in the final generation or to average the last two or three generations; and there were other uncertainties. The values in Table 2 are therefore not definitive, and must be recognized as being only approximations. Nevertheless, with 13 experiments or replicates of upward selection and 8 of downward

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Table 1. *Sources and description of data in Tables 2, 4, and 6, giving* (i) *the character selected,* (ii) *the environment, high* vs. *low,* (iii) *whether the means and phenotypic variances before selection were obtained from the base population or from an unselected contemporaneous control,* (iv) *whether the heritabilities and genetic correlation were estimated from the base population or as realized in the selection lines,* (v) *replication*

Nicotiana rustica

(1) Mather & Jinks (1982), tables 42 and 44
(i) Final plant height. (ii) Combinations of sowing date and planting density. No selection applied; all parameters calculated directly from values of genotypes.

Schizophyllum commune (a heterothallic basidiomycete)

(2) Jinks & Connolly (1973)
(i) Growth rate of mycelium. (ii) Temperature, 30 *vs.* 20 °C. (iii) Control. (v) The two 'replicates' in Tables 2, 4 and 6 are from different base populations, each being the mean of 4 replicates.

Mice

(3) Falconer & Latyszewski (1952)
(i) 6-week weight. (ii) Diet: normal *ad lib. vs.* reduced amount. (iii) Parameters after one generation of selection.

(4) Falconer (1960)
(i) 3- to 6-week growth. (ii) Normal *vs.* diluted diet fed *ad lib.* (iii) Control. (iv) Realized.

(5) Nielsen & Andersen (1987)
(i) 3- to 6-week growth. (ii) Normal *vs.* reduced-protein diet. (iii) Control. (iv) Realized. (v) 3 replicates shown separately in Table 2, combined in Tables 4 and 6.

(6) Lynch, Sulzbach & Connolly (1988)
(i) Nest-building: weight of nesting material used in 4 days, transformed to square roots. (ii) Temperature, 4 *vs.* 21 °C. (iii) Heritabilities and genetic correlation from offspring–parent regression; all parameters pooled within sexes. No selection applied.

Pigs

(7) Fowler & Ensminger (1960)
(i) Daily weight gain from weaning to 150 lb. (ii) Diet: normal *ad lib. vs.* reduced amount. (iii) Base.

Tribolium

(8) Yamada & Bell (1969)
(i) 13-day larval weight. (ii) Nutritional value of food. (iii) Base. (iv) Base. (v) 2 replicates.

(9) Orozco (1976)
(i) Number of eggs laid in 4 days. (ii) 3 temperatures, treated here as 3 experiments with 2 environments: Normal (N) at 33 °C, Cold stress (C) at 28 °C, and Heat stress (H) at 38 °C. (iii) Base. (iv) Base. (v) 2 replicates, here combined.

selection, we can get a good idea of how selection affected the sensitivity and the mean performance.

Consider sensitivity first. Putting the two directions of selection together, there are 21 antagonistic selections and 21 synergistic selections. Antagonistic selection decreased sensitivity in 14 cases, and synergistic selection increased it in 16 cases. Thus 30 selected lines out of 42 conformed to the Jinks–Connolly rule and 12 were exceptions to it. It is possible that many, or indeed all, of the exceptions are due to errors in the parameters estimated, particularly of the environmental effect, D, in the base population. We shall see later from the theory that there are circumstances in which the rule is not expected to hold and it therefore cannot be regarded as a general principle. A modified version of the rule, however, is true in all of the 21 comparisons in Table 2; this is that the sensitivity is less after antagonistic than after synergistic selection.

Now consider the means. Antagonistic selection was better than synergistic selection for increasing the mean in 8 of 13 cases, and for decreasing it in 6 of 8 cases. Putting the two directions of selection together we have 14 cases where antagonistic was better, 5 where synergistic was better, and 2 where the two were equal. The ratio 14:5 is significantly different from 1:1 ($\chi^2_{[1]} = 4{\cdot}26$, $P = 0{\cdot}039$). The unweighted mean and empirical standard error of the 21 values is $1{\cdot}29 \pm 0{\cdot}12$, which is significantly different from 1·0 ($P = 0{\cdot}022$). There does therefore seem to be some practical justification for thinking that antagonistic selection is better than synergistic selection for changing the mean performance. We shall see, however, that, as a prediction, this has no justification in theory.

4. Theory

(i) *Configurations of sensitivities*

The genetic correlation and other parameters depend on how the sensitivities of individuals intersect. Fig. 3 shows the configurations that result in a genetic correlation of $+1$ or -1. The correlation is obviously $+1$ if there are no differences of sensitivity; the lines representing sensitivities are parallel and do not intersect (A in Fig. 3). The correlation is $+1$ or -1 if all the sensitivities intersect at a single point; it is $+1$ if the point of intersection is outside the range of environments (B and C), and -1 if the point of intersection is between the two environments (D). A single point of intersection seems very improbable in reality, but it could arise from a scale effect, particularly in B. If a scale transformation were made to equalize the variances in the two environments, this might eliminate differences of sensitivity on the transformed scale. Scale effects will be examined later.

Consider now just two genotypes. Fig. 4 shows all the ways in which their sensitivities may intersect. The four configurations are in principle distinguishable by the variances in the low and high environments and the genetic correlation. In A and C, where the intersections are below the mid-environment, the variance is less in the low environment than in the high; in B and D, where the intersection is above the mid-environment, it is greater. A and C differ from B

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Table 2. *Observed sensitivities after antagonistic (Ant.) and synergistic (Syn.) selection (initial sensitivity = 1·0), and relative merits of antagonistic* vs. *synergistic selection for changing the mean performance (equal merit = 1·0). Sources of data are in Table 1*

			Sensitivity				Response of mean	
			Up		Down		Ant./Syn.	
Source	Gen.	Rep.	Ant.	Syn.	Ant.	Syn.	Up	Down
Schizophyllum								
(2)	8	(i)	0·8	1·2	0·2	0·6	0·8	1·1
		(ii)	1·3	1·4	0·1	0·6	1·0	1·3
Mice								
(3)	7	—	1·3	2·0	—	—	1·4	—
(4)	7	—	0·6	1·4	1·0	1·5	1·6	1·3
(5)	5	(i)	0·3	1·9	0·8	1·2	2·0	0·8
		(ii)	1·2	1·4	0·7	1·9	1·2	3·2
		(iii)	0·8	1·1	0·4	1·6	1·4	1·6
Pigs								
(7)	6	—	1·1	1·3	—	—	1·2	—
Tribolium								
(8)	16	(i)	0·2	1·0	0·5	0·9	1·2	0·8
		(ii)	0·5	1·1	−0·2	0·7	1·2	1·2
(9)	20	N-C	3·5	4·6	—	—	0·9	—
		N-H	1·6	4·6	—	—	1·0	—
		H-C	−2·0	15·7	—	—	0·8	—

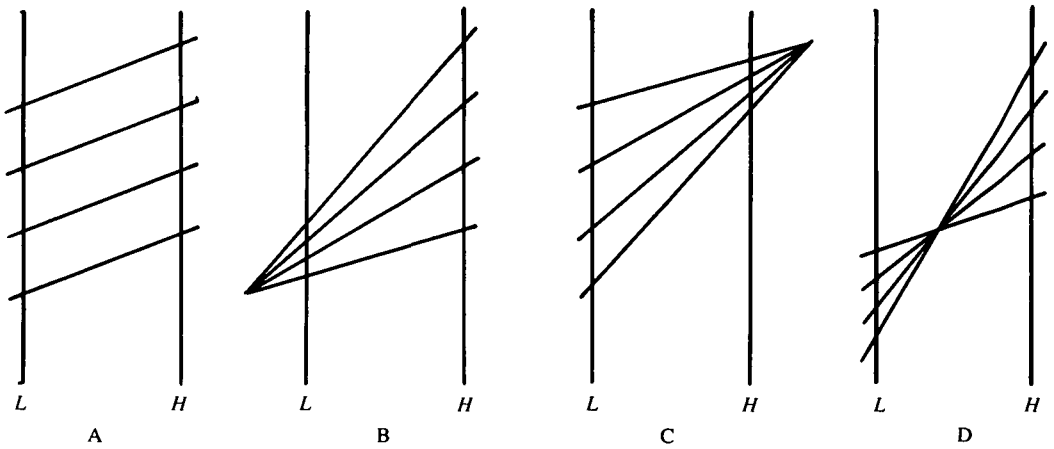

Fig. 3. Configuration of sensitivities that give genetic correlations of +1 or −1.

and D also in the correlation between sensitivity and mean performance, which is positive in A and C and negative in B and D. The genetic correlation differentiates A and B from C and D, being positive in A and B and negative in C and D.

In a real population with many genotypes all the configurations in Fig. 4 are likely to be represented, and the parameters will depend on which configuration is predominant. Intersections within the environmental range (C and D) contribute negatively to the covariance of performance in the two environments and so are the chief cause of low genetic correlations. If the genetic correlation is high we can conclude that not many sensitivities intersect between the two environments, which means that not many pairs of genotypes reverse their order in the two environments. The 10 *Nicotiana* genotypes in Fig. 1 have the following parameters, calculated directly from the data. The variance is less in the low environment than in the high (297 *vs.* 360 cm²); the correlation between sensitivity and mean is positive (+0·25); and the genetic correlation between performances in the two environments is high (+0·93). From these parameters we would expect A in Fig. 4 to be the predominant configuration of intersections. Actually, of the 45 intersections, 22 are of type A, 15 of B, 5 of C, 2 of D, and one pair do not intersect because they have the same sensitivity. So, as expected, A is the predominant configuration, and there are few intersections within the environmental range. It may be worth noting also

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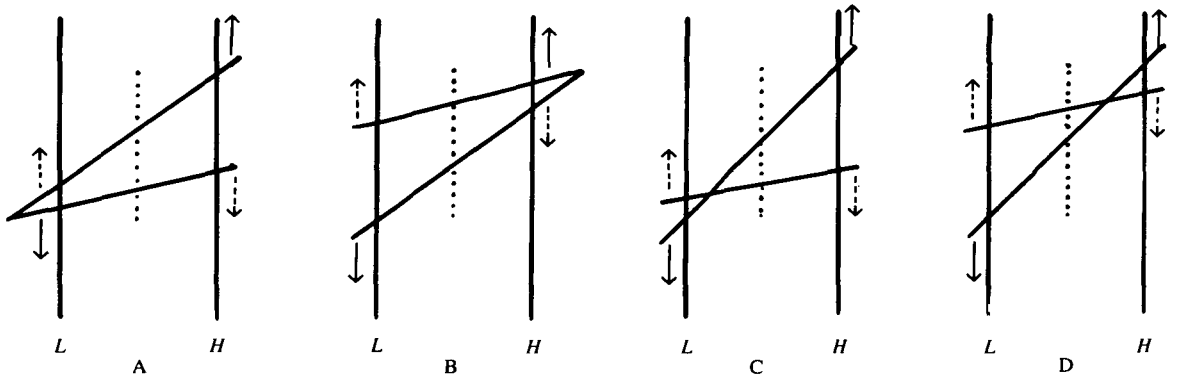

	A	B	C	D
V_G:	$L < H$	$L > H$	$L < H$	$L > H$
r_{MS}:	+ ve	− ve	+ ve	− ve
r_G:	+ ve	+ ve	− ve	− ve

Fig. 4. Configurations of sensitivities of two genotypes, showing the consequences of selection. Broken arrows are antagonistic selection; solid arrows are synergistic selection. The vertical dotted lined marks the mean performance in the two environments.

that, because of the high genetic correlation, there is very little $G \times E$ intersection variance; it accounts for only 3% of the total variance due to the 10 genotypes and 8 environments.

Fig. 4 shows also the consequences of selecting between the two genotypes. With configurations A and B antagonistic and synergistic selection will both select the same genotype, and this is true of both upward and downward selection. With configurations C and D antagonistic and synergistic selection will select different genotypes, but each type of selection selects the same genotype irrespective of the direction of selection.

The changes of sensitivity resulting from selection in one or other environment differ according to the configuration and the type and direction of selection. In A upward selection of both types leads to increased sensitivity and downward selection to reduced sensitivity; in B the consequences are reversed. In C and D antagonistic selection in both directions leads to a reduced sensitivity and synergistic selection to an increased sensitivity. This is the Jinks–Connolly rule. Populations will, however, almost never consist entirely of configurations C and D. If configuration A or B predominated, sensitivity might be changed in the same way by both types of selection. It seems from these rather simple considerations, therefore, that the rule may not be true in all circumstances. This suggests that some of the exceptions shown by the experiments in Table 2 may be real. We shall see later what are the circumstances in which the rule is expected not to hold.

In their effects on the mean performance the two types of selection differ only in configurations C and D, where the intersections are within the environmental range. When the intersection is below the mid-environment, in C, synergistic selection is better for increasing the mean and antagonistic for reducing it. When the intersection is above the mid-environment, in D, the situation is reversed. Thus there seems to be no theoretical basis for the idea that antagonistic selection is the better way of both increasing and decreasing the mean performance. The expected responses will now be examined more rigorously.

(ii) *Predicted responses*

The changes of mean and sensitivity following selection in one or other environment can be predicted from parameters estimated in the base population. The change of mean is the average of the direct response (R) in one environment and the correlated response (CR) in the other environment. The change of sensitivity is the difference between these two responses divided by the environmental effect, D. Direct and correlated responses are both predictable from a knowledge of the intensities of selection, the heritabilities, the genetic correlation, and the variances. See equations (11·4) and (19·5*b*) of Falconer (1989). The expected changes are set out in Table 3. They can be verified by consideration of the responses in Fig. 2. The downward responses are assumed to be given negative signs. The expected change of the mean here is equivalent to the expression derived by James (1961).

What do these expressions tell us? Consider first the mean. The expected responses for upward and downward selection are the same because there is no asymmetry in the expectations. But in each environment selection in one direction is antagonistic and selection in the other direction is synergistic. (Synergistic responses are in bold type in Table 3.) Antagonistic and synergistic selection in the same direction have different expectations. Therefore if one type of selection is better for changing the mean in one direction it cannot be better for changing it in the other direction. This is proof of the conclusion reached earlier by consideration of two genotypes in Fig. 4.

Now consider the sensitivity. The expressions are again the same in the two directions. But, because the

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Table 3. *Response of mean and of sensitivity to selection in low or high environments. R and CR are direct and correlated responses respectively; the subscript is the environment in which the response is measured. Responses to synergistic selection are in* ***bold*** *type. Downward responses have negative signs*

	Response of mean		Response of sensitivity	
	Environment of selection		Environment of selection	
	Low	High	Low	High
Up	$\frac{1}{2}(R_L+CR_H)$	$\frac{1}{2}(\mathbf{R_H}+\mathbf{CR_L})$	$(CR_H-R_L)/D$	$(\mathbf{R_H}-\mathbf{CR_L})/D$
Down	$\frac{1}{2}(\mathbf{R_L}+\mathbf{CR_H})$	$\frac{1}{2}(R_H+CR_L)$	$(\mathbf{CR_H}-\mathbf{R_L})/D$	$(R_H-CR_L)/D$

responses downward are negative, the changes of sensitivity are very different in the two directions. Antagonistic selection will reduce sensitivity and synergistic selection increase it (the Jinks–Connolly rule) if the direct response in the environment of selection is greater than the correlated response in the other environment. That is, for antagonistic selection upwards, if

$$R_L > CR_H$$

and, for synergistic selection upwards, if

$$R_H > CR_L.$$

The circumstances under which the rule would be broken, expressed in terms of the additive genetic parameters, are

$$\sigma_L < r_A \sigma_H$$

for antagonistic selection and

$$\sigma_H < r_A \sigma_L$$

for synergistic selection. A large difference in the additive variances in the two environments coupled with a high genetic correlation could result in antagonistic selection increasing sensitivity or synergistic selection reducing it. The Jinks–Connolly rule is therefore not true in principle, and the conditions under which it would be broken do not seem very improbable. Whether the 12/42 exceptions in Table 2 were real or were due to errors of estimation cannot be decided.

The modified rule, that sensitivity is less after antagonistic than after synergistic selection, requires that

$$(R_H-CR_L)-(CR_H-R_L) > 0$$

or

$$(R_H+R_L) > (CR_H+CR_L).$$

It is thus not necessary that both direct responses should be greater than their corresponding correlated responses; only that the sum of the direct responses should be greater than the sum of the correlated responses. This condition is much less likely to be violated than the condition for the Jinks–Connolly rule itself, and there were no exceptions to the modified rule in Table 2.

Table 4. *Proportion of total response due to change of mean performance observed after selection upwards in the high environment (synergistic). Predicted values, obtainable for only two experiments, are in parentheses (for sources see Table 1)*

Source	Generations	Replicate	R_M/R_T (%)	
Schizophyllum				
(2)	8	(i)	73	
		(ii)	68	
Mice				
(3)	7		49	
(4)	7		64	(89)
(5)	5	Mean of 3	58	(69)
Pigs				
(7)	6		76	
Tribolium				
(8)	16	(i)	99	
		(ii)	95	
(9)	20	N-C	83	
		N-H	92	
		H-C	81	

It might be of interest to know how much of the total response is due to a change of mean performance and how much to a change of sensitivity. The total response, R_T, is

$$R_T = R_M \pm \tfrac{1}{2} D R_S,$$

where R_M and R_S are the changes of mean and sensitivity respectively, as given in Table 3; the + sign refers to synergistic selection and the − sign to antagonistic selection. Unfortunately only two of the sources give the data needed to predict the responses. We can, however, look at what actually happened. The observed proportion of the total response due to a change of mean after upward selection in the high environment (synergistic) is given in Table 4. The proportion due to the change of mean ranged from 49 to 99%. The experiments with *Tribolium*, which were

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continued for longer periods, show higher proportions due to the change of mean. The predictions, which could be made for two experiments, are shown in parentheses. In both cases more change of mean and less of sensitivity was predicted than was observed.

There is one further point about selection to be noted. The environmental effect, D, evaluated from the selected populations may not be the same as it was when evaluated in the base population, for the following reason. Consider two lines selected upwards, one by antagonistic and the other by synergistic selection. The environmental effect would be estimated as the difference between the mean of the lines in the high environment and the mean of the lines in the low environment. Let D_0 be the environmental effect in the base population and D_t the effect estimated from the selected lines. It can be shown by reference to Fig. 2 that

$$D_t = D_0 + \tfrac{1}{2}[(R_H + CR_H) - (R_L + CR_L)].$$

The selected lines will show the same environmental effect as the base population only if the sums of the two responses are the same in each environment, which is a rather unlikely event. In the experiments in Table 2 the ratio D_t/D_0 ranged from 0·2 to 6·8, upward selection leading more often to an increase of D and downward selection to a decrease.

(iii) *Relationships between parameters*

In this section we are concerned with the properties of any population, and not with the responses to selection. The characteristics of an individual can be described by two parameters, its mean performance, M, and its sensitivity, S. Let X_H and X_L be the performances of the individual in the high and low environments respectively, or would be the performances if they could both be measured in the same individual. Then the individual's mean is

$$M = \tfrac{1}{2}(X_H + X_L)$$

and its sensitivity is

$$S = (X_H - X_L)/D,$$

where

$$D = \bar{X}_H - \bar{X}_L,$$

i.e. the difference between the means of all individuals in the high and in the low environments.

The corresponding population parameters are the variance of means, V_M, the variance of sensitivities, V_S, and the covariance of means and sensitivities, cov_{MS}. The means and sensitivities of individuals are seldom observable because the measurement of an individual in one environment usually precludes its measurement in the other environment. Usually, therefore, these population parameters cannot be directly estimated. Another set of three parameters is the variance in the high environment, V_H, the variance in the low environment, V_L, and the covariance of performance in the two environments cov_{HL}. The first two of these are directly observable but the phenotypic covariance is not, for the same reason as before. I shall nevertheless call this second set the observable parameters, the first set being the population parameters. Our purpose here is to express the observable parameters in terms of the population parameters and vice versa. These relationships are given in Table 5. Equations (1)–(3) in the table show how the observable parameters are made up of the population parameters, and equations (4)–(6) show how the population parameters can be indirectly estimated from the observable parameters. The derivations of these equations are given in the Appendix. There is no genetics in these derivations; the equations are all derived by the manipulation of variances and covariances. Consequently the relationships apply equally to phenotypic, genotypic, or additive genetic, variances and covariances. In practice, however, they are usually restricted to additive genetic values because this is usually the only estimate of cov_{HL} that can be obtained; it is of course related to the genetic correlation by $\mathrm{cov}_{(A)HL} = r_A \sigma_{(A)H} \sigma_{(A)L}$.

We may now ask what useful or interesting information can be got from the relationships in Table 5. One interesting thing would be to find out how much of the observed variance in one or other environment is due to the variance of means and how much to the variance of sensitivities and the covariance of means and sensitivities. The reports of six experiments give the data needed, and the results are shown in Table 6, together with the observed parameters from which they were derived. The parameters are all additive genetic except for *Nicotiana* for which they are genotypic, as explained in connection with Fig. 1, and one mouse experiment from which phenotypic parameters were obtained. The values of V_M, V_S, and cov_{MS} were first calculated by equations (4)–(6) of Table 5, and the contributions of these to V_H were then calculated by equation (1). In order to make the results comparable, V_M was here set at 100 and the other parameters scaled accordingly as percentages. Also given in Table 6 are the correlations between performances in the two environments, r_{HL}, and the correlations between mean and sensitivity, r_{MS}.

The points of interest that emerge from Table 6 are: (i) In all cases V_M contributes more to the variance in the high environment than do V_S and cov_{MS} together; (ii) In the *Nicotiana* experiment, where the genetic correlation is very high, nearly all the variance comes from V_M; (iii) The genetic cov_{MS} is positive in all except the three mouse experiments, which means that configurations B and D of Fig. 4 were predominant in the mouse experiments, but A and C in all the others.

Experiment (6) in Table 6 was on nest-building in mice. This character can be measured on individuals in both environments, and so the phenotypic parameters can be obtained; they are underlined in the

Table 5. *Relationships between parameters, genotypic, or additive genetic. V_H and V_L are the variances of performance in the high and low environments respectively, and cov_{HL} is the corresponding covariance. D is the difference between the mean performances in the high and low environments*

$V_H = V_M + \frac{1}{4}D^2V_S + D\,\text{cov}_{MS}$,	(1)	$V_M = \frac{1}{4}(V_H + V_L) + \frac{1}{2}\text{cov}_{HL}$,	(4)
$V_L = V_M + \frac{1}{4}D^2V_S - D\,\text{cov}_{MS}$,	(2)	$V_S = (V_H + V_L - 2\,\text{cov}_{HL})/D^2$,	(5)
$\text{cov}_{HL} = V_M - \frac{1}{4}D^2V_S$,	(3)	$\text{cov}_{MS} = (V_H - V_L)/2D$,	(6)

Table 6. *Parameters in the unselected populations. The variances, covariances and correlations are additive genetic except where noted on the left*

Source	V_H*	V_L*	V_M	$\bar{M}$*	D*	r_{HL}*	r_{MS}	Components of V_H: V_M	$\frac{1}{4}D^2V_S$	$D\,\text{cov}_{MS}$
Nicotiana										
(1) Genotypic	360	297	314	115	29	0·93	0·25	100	4	10
Mice										
(4)	0·74	1·91	0·95	12·1	2·6	0·48	−0·49	100	40	−62
(5)	1·28	1·78	1·01	11·5	2·0	0·33	−0·17	100	51	−24
(6)	0·34	0·53	0·39	4·9	1·8	0·83	−0·37	100	10	−24
(6) Phenotypic	1·10	1·00	0·78	4·9	1·8	0·49	+0·06	100	34	+7
Tribolium										
(8) (i)	430	286	323	171	112	0·82	0·34	100	11	22
(ii)	805	377	511	169	103	0·78	0·53	100	16	42
(9) N-C	57·1	20·2	33·9	15·7	5·6	0·86	0·73	100	14	54
N-H	57·1	47·5	44·1	16·7	3·7	0·68	0·13	100	19	11
H-C	47·5	20·2	29·1	13·8	1·9	0·79	0·58	100	16	47

Parameters marked by asterisks are observed; the rest are calculated by the equations in Table 5. The three right-hand columns give the composition of the genetic variance in the high environment from equation (1), scaled to $V_M = 100$. The sources and other details are in Table 1.
The units are: (1), cm; (4), (5), g; (6), $g^{\frac{1}{2}}$; (8), 10^{-2} mg; (9), egg number.

table. We can accordingly estimate the heritabilities of mean performance and of sensitivity from the ratio of additive to phenotypic variance. The values obtained are as follows, with the heritabilities in the two environments for comparison:

h^2_H	h^2_L	h^2_M	h^2_S
0·31	0·53	0·50	0·15

(iv) *Scale*

Many characters have higher variances when the means are higher. In all the experiments analysed in Table 6, except the mouse ones, the variance was higher in the high than in the low environment. One wonders therefore if the difference of variance could be a scale effect associated with the difference of mean. How would a scale effect influence the parameters as estimated in the previous section? For example, with configurations B and C in Fig. 1 or A and B in Fig. 2, some of the variation of sensitivity might be ascribable to a scale effect, and some of the response of sensitivity to selection might be due to the change of mean rather than to a real change of 'buffering' or 'canalization'. How can we decide if a scale effect is causing variation of sensitivity?

Let us consider just one simple situation: a character such as body size, with multiplicative combination of factors influencing it and a constant coefficient of variation. A log-transformation would then equalize the variance in the two environments. If there was no variation of sensitivity other than that due to the scale effect, then the variance of sensitivity calculated from untransformed values would be

$$V_S = V_M/\bar{M}^2, \quad (7)$$

where V_M is the variance of mean performances and $\bar{M}$ is the overall mean performance. (The derivations of this and subsequent equations are given in the Appendix.) If the observed variance of sensitivity, calculated from equation (5), is less than this it cannot be due to a logarithmic scale effect; if the observed variance is more, then the excess would be ascribable to real differences of sensitivity.

Now consider the covariances. Calculated from untransformed values these would be

$$\text{cov}_{MS} = V_M/\bar{M}, \quad (8)$$

$$\text{cov}_{HL} = V_M. \quad (9)$$

The correlations, r_{MS} and r_{HL} would both be equal to +1. Thus a high genetic correlation together with a

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high correlation of mean and sensitivity would be an indication of a logarithmic scale effect.

Finally consider changes of sensitivity following selection. The change of sensitivity expected as a scale effect consequent on a change of mean is as follows. Letting subscripts 0 and t refer to the population before and after selection respectively, then

$$S_t/S_0 = M_t/M_0.$$

By definition $S_0 = 1{\cdot}0$, so the final sensitivity expected as a scale effect associated with the change of mean is

$$S_t = M_t/M_0. \qquad (10)$$

This expression will be used in the Discussion.

In all the experiments in Table 6 the variance of sensitivity was less, and often much less, than would be expected by equation (7) from a logarithmic scale effect, so we can conclude that in no case was the variance of sensitivity ascribable to a logarithmic scale effect. We must ask, however, whether a scale effect other than the logarithmic one considered was causing variation of sensitivity. Any association between sensitivity and mean performance could properly be ascribed to a scale effect. The square of the correlation would then estimate the proportion of the variance that is associated with differences of mean performance, and $(1 - r^2_{MS})$ would estimate the proportion due to differences of 'real' sensitivity not associated with the mean. Applying this to the experiments in Table 6 we could conclude that between 47 and 98% of the additive (or genotypic) variance was variation of 'real' sensitivity, the rest being due to a scale effect of some sort. Whether this would be a meaningful conclusion, however, is problematical, as can be seen from experiment (6). This was on nest-building in mice. The measurements were transformed to square roots before analysis because this transformation rendered the distribution symmetrical and equalized the phenotypic variance in the two environments. But the transformation 'over-corrected' the additive variance, making it greater in the low than in the high environment. The values of r^2_{MS} are 0·004 for phenotypic values and 0·137 for additive values. So, after the square-root transformation the phenotypic variance of sensitivity was independent of the mean, and thus all 'real', but 14% of the additive variance was associated with the mean, leaving only 86% as 'real'. No single scale transformation could make both the phenotypic and the additive values independent of the mean. This might well be true also of other characters, and in these circumstances it is far from clear how a scale effect should be interpreted.

Whether the phenomena displayed by scale-transformed or by untransformed data are considered the more biologically meaningful generally depends on personal opinion. Nevertheless, it does seem necessary to consider scale effects in connection with sensitivity. If the correlation between mean and sensitivity (r_{MS}) was found to be very high, this would mean that most of the variation of sensitivity was associated with differences of mean performance. Sensitivity could then be changed very little by selection without also changing the mean; and, conversely, any change of mean brought about by selection would inevitably be accompanied by a change of sensitivity.

5. Discussion

(i) *Sensitivity*

The changes of sensitivity brought about by selection in the experiments reviewed agree well with theoretical expectations. The Jinks–Connolly rule, that antagonistic selection decreases sensitivity and synergistic selection increases it, is not expected to be true in all circumstances, and there were 12 exceptions to it in 42 selected lines. The modified rule, that sensitivity is less after antagonistic than after synergistic selection, is expected to be true in all but very unlikely circumstances, and there was no exception to it in 21 comparisons of antagonistic and synergistic selection. The modified rule is another way of saying that direct responses are in general greater than correlated responses; or, alternatively, that for improving performance in one environment selection should be made in that environment. This is a generally accepted principle, borne out by many experiments. In addition to the experiments reviewed here there are others, not reviewed because they did not provide the necessary data, that also bear it out. They are: body size of mice on two diets (Korkman, 1961); larval weight of *Tribolium* in wet and dry environments (Friars *et al.* 1971); body size of *Drosophila* after culture in normal or low-protein media (Robertson, 1960); wing length at different temperatures (Druger, 1962); growth of broiler chickens on different diets (Sørensen, 1980); various measures of the yield of sugar cane grown in high- and low-yielding localities (Simmonds, 1984). Three experiments, however, gave anomalous results, no differences being detected between direct and correlated responses, and the realized genetic correlations being in consequence estimated as 1·0. The anomalous experiments are: mice selected for 3–6 weeks' growth on a normal diet and one diluted by 70% cellulose (Dalton, 1967); rats selected for 3–9 weeks' growth on three diets, normal, restricted intake, and low-protein (Park *et al.*, 1966); mice selected for feed efficiency on normal diet and restricted intake (Yüksel, Hill & Roberts, 1981).

(ii) *Mean*

The idea that mean performance will be changed most, in either direction, by antagonistic selection has no justification in theory. The theoretical expectation is that if one type of selection is best for increasing the mean, then the other type of selection will be best for decreasing it. So antagonistic selection has no ad-

vantage in theory except for the reduced environmental sensitivity, which may itself be desirable. Yet the experiments reviewed in Table 2 showed antagonistic selection to be significantly better than synergistic selection. We might regard this superiority, despite its formal significance, as an aberrant result without a real basis. There is, however, a possible reason for it. The theoretical prediction takes no account of the asymmetry in the responses to selection which is frequently found in selection experiments. It is possible that a prevalent pattern of asymmetry could be the cause. The asymmetries that would make antagonistic selection better than synergistic in both directions can be deduced from the responses of the mean in Table 3, but they are very complicated because there are four asymmetries to be considered, those of the direct and the correlated responses in the high and the low environments. If a greater response upward than downward is counted as positive asymmetry then, briefly and without proof, it seems that the asymmetries must be greater in the low environment than in the high, and that these differences must be greater for correlated than for direct responses. It is not clear to me, however, why this pattern of asymmetries should occur more commonly than any other pattern. Some doubt must therefore remain about whether the observed superiority of antagonistic selection is a real phenomenon.

(iii) *Directional and stabilizing selection in one macro-environment*

This paper has been concerned with macro-environments, differing by identified physical factors artificially imposed. The conclusions about how selection affects sensitivity are, however, relevant also to selection in a single macro-environment, both to directional and to stabilizing selection. In a single macro-environment there are unidentified and naturally occurring factors that cause environmental variation of the character selected. The sensitivity to these environmental factors is affected in the same way by selection as is the sensitivity to macro-environmental factors, and, if there is any genetic variation of sensitivity, the mean sensitivity will be expected to change as a result of the selection.

Directional selection based on phenotypes (i.e. individual selection) is synergistic with respect to the unidentified environmental factors. The individuals selected are those that have experienced a favourable environment and have the genetic ability to perform well in that environment. Consequently sensitivity should be increased by directional selection, and the increased sensitivity will be seen in an increased environmental component of variance. Selection experiments provide evidence of this expected increase of environmental variance. In many experiments the heritability has been found to decline while the phenotypic variance has not declined, or has even increased. This can only mean that the environmental variance has increased.

Stabilizing selection, on the other hand, is antagonistic with respect to the unidentified environmental factors; and moreover it is antagonistic selection in both directions at the same time. Individuals with a high phenotypic value owe their high value partly to having experienced a high environment; they are selected downwards. And, conversely, those with a low value have experienced a low environment and they are selected upwards. Stabilizing selection should therefore result in a reduction of environmental sensitivity and so of environmental

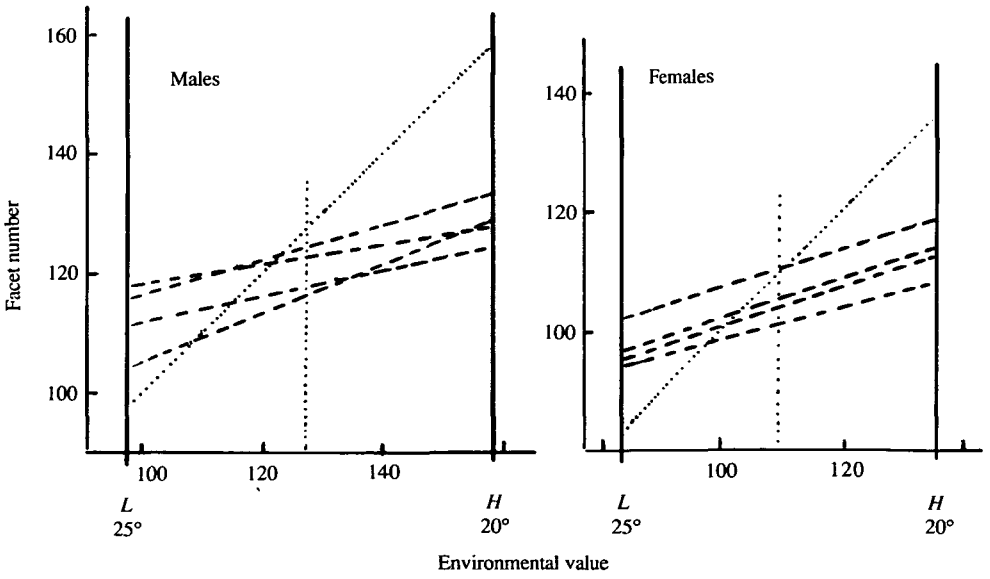

Fig. 5. The consequences of 14 generations of stabilizing selection for facet number in Bar-eyed *Drosophila*. Four replicate selection lines are shown by broken lines, and the base population by the sloping dotted line. The mean performance is marked by the vertical dotted line. Data from Thompson & Rook (1988).

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Table 7. *Stabilizing selection for facet number in* Drosophila (*Thompson & Rook, 1988*). *Sensitivities after selection expected from a logarithmic scale effect, and observed, as explained in the text*

	Males	Females
M_0	127·65	109·40
M_t	120·63	105·15
Expected S_t	0·945	0·961
Observed S_t	0·24 ± 0·045	0·30 ± 0·013

variance. There is evidence that supports this expectation from several laboratory experiments; see Kaufman *et al.* (1977).

There is also a recent experiment on stabilizing selection in two macro-environments which provides very clear evidence of reduced sensitivity. This is an experiment on *Drosophila* by Thompson & Rook (1988), which is worth describing in some detail. The character was the number of facets in the eyes of Bar-eyed mutants reared at two temperatures, 20 and 25 °C. The number of facets is reduced by higher rearing-temperatures, so 20 °C was the 'high' environment in the terminology of this paper. The population was divided in two parts, one part being reared in the high environment and the other in the low environment. Those reared in the high environment were selected for low facet number, and those reared in the low environment were selected for high facet number. The selected individuals were then bred as a single population. Thus the population was subjected to antagonistic selection both upwards and downwards. There were 4 replicates and the sexes were scored separately. The sensitivities of the base population and of the four replicates after 14 generations of selection are shown in Fig. 5. The initial sensitivity was 1·0 by definition. The average sensitivity of the replicates after selection was 0·24 in males and 0·30 in females. The means were a little lower after selection than before. Facet number has a skewed distribution which is rendered approximately normal by a log-transformation (see Falconer, 1989, p. 106). We should therefore ask if the reduced sensitivity could have been a scale effect associated with reduced mean. Table 7 gives: the means before and after selection; the sensitivities after selection expected from a logarithmic scale effect, by equation (10); and the sensitivities observed, with empirical standard errors based on the samples of 4 replicates. Clearly, the scale effect cannot have made more than a very small contribution to the reduction of sensitivity resulting from the stabilizing selection. We must conclude therefore that stabilizing selection caused a real reduction of environmental sensitivity.

(iv) *Fitness*

How would fitness be affected by the changes of sensitivity expected from the foregoing considerations? To answer this question we would need to know whether the sensitivity was adaptive or non-adaptive and, if adaptive, whether it was at its optimal level. Adaptive sensitivity, better called plasticity, is itself a component of fitness; non-adaptive sensitivity affects fitness only through its effect on the phenotype of the character.

Nest-building of mice in different temperatures is an adaptive sensitivity; building larger nests in the cold is clearly an adaptive response which increases fitness. This is a character whose sensitivity is subject to direct selection in individuals, because individuals may encounter a different environment every time they build a nest. We should therefore expect sensitivity to be at an optimal level in wild populations. Any change of sensitivity would then reduce fitness.

Non-adaptive sensitivity is exemplified by body weight of mice fed different diets, or egg-laying by *Drosophila* in different temperatures, though perhaps neither of these is entirely non-adaptive. If the character itself has an intermediate optimum and is subject to stabilizing selection then the reduced sensitivity would be advantageous to individuals. If the character is subject to directional selection, the increased sensitivity expected would be beneficial to those individuals that experienced a good (high) environment, but detrimental to those that experienced a bad (low) environment. Any change of sensitivity might therefore have very little effect on the mean fitness.

The effect of sensitivity or plasticity on fitness is a complicated matter and cannot be considered further here. Via & Lande (1985) present models describing the evolution of plasticity.

I am indebted to Professor S. C. Stearns for his invitation to participate in a symposium on reaction norms, which led to the writing of this paper. Professors W. G. Hill, R. C. Roberts and Carol B. Lynch read the draft and I am very grateful for their comments and suggestions.

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Appendix

(The equations are numbered as in Table 5 and the text.)

(i) *Equations in Table 5*

Let X_H and X_L be the values of individuals in the high and low environments respectively, and let X_M be the mean of X_H and X_L. D is the environmental effect measured as the difference of means $\bar{X}_H - \bar{X}_L$. S is the individual sensitivity defined as $(X_H - X_L)/D$. Then

$$X_H = X_M + \tfrac{1}{2}DS$$

and

$$X_L = X_M - \tfrac{1}{2}DS.$$

So the variance in the high environment is

$$V_H = V_M + \tfrac{1}{4}D^2V_S + 2\,\mathrm{cov}_{(X_M \cdot \frac{1}{2}DS)}$$
$$V_H = V_M + \tfrac{1}{4}D^2V_S + D\,\mathrm{cov}_{MS}. \quad (1)$$

Similarly the variance in the low environment is

$$V_L = V_M + \tfrac{1}{4}D^2V_S - D\,\mathrm{cov}_{MS}. \quad (2)$$

Subtracting (2) from (1) gives

$$V_H - V_L = 2D\,\mathrm{cov}_{MS},$$

whence

$$\mathrm{cov}_{MS} = (V_H - V_L)/2D. \quad (6)$$

The mean of an individual is

$$X_M = \tfrac{1}{2}(X_H + X_L),$$

so the variance of means is

$$V_M = \tfrac{1}{4}(V_H + V_L + 2\,\mathrm{cov}_{HL})$$
$$V_M = \tfrac{1}{4}(V_H + V_L) + \tfrac{1}{2}\mathrm{cov}_{HL}, \quad (4)$$

where cov_{HL} is the covariance of X_H with X_L.

This covariance can be written as

$$\mathrm{cov}_{HL} = \mathrm{cov}(X_M + \tfrac{1}{2}DS)(X_M - \tfrac{1}{2}DS)$$
$$\mathrm{cov}_{HL} = V_M - \tfrac{1}{4}D^2V_S. \quad (3)$$

The sensitivity of an individual is

$$S = (X_H - X_L)/D,$$

so the variance of sensitivities is

$$V_S = (V_H + V_L - 2\,\mathrm{cov}_{HL})/D^2. \quad (5)$$

(ii) *Scale*

Let the values on the untransformed scale be as follows. For any individual, $X_H = kM$ and $X_L = M/k$, where k is the constant of proportionality and M is the individual's mean performance. Similarly the population means are $\bar{X}_H = k\bar{M}$ and $\bar{X}_L = \bar{M}/k$, where $\bar{M}$ is the overall population mean performance. Then the environmental effect is

$$D = k\bar{M} - (\bar{M}/k).$$

The sensitivity of an individual is

$$S = (X_H - X_L)/D$$
$$= (kM - M/k)/(k\bar{M} - \bar{M}/K)$$
$$= M/\bar{M}$$

and the variance of sensitivity is

$$V_S = V_M/\bar{M}^2 \quad (7)$$

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The covariance of mean and sensitivity is

$$\begin{aligned} \mathrm{cov}_{MS} &= \mathrm{cov}_{(M \cdot M/\bar{M})} \\ \mathrm{cov}_{MS} &= V_M/\bar{M} \end{aligned} \tag{8}$$

and the correlation is

$$\begin{aligned} r_{MS} &= (V_M/\bar{M})/(\sigma_M \sigma_S) \\ &= (V_M/\bar{M})/(\sigma_M \sigma_M/\bar{M}) \\ &= 1. \end{aligned}$$

The covariance of values in the two environments is

$$\begin{aligned} \mathrm{cov}_{HL} &= \mathrm{cov}_{(kM \cdot M/k)} \\ \mathrm{cov}_{HL} &= V_M. \end{aligned} \tag{9}$$

The variances in the two environments are

$$V_H = k^2 V_M \quad \text{and} \quad V_L = V_M/k^2,$$

so the correlation is

$$\begin{aligned} r_{HL} &= V_M/(k\sigma_M \sigma_M/k) \\ &= 1. \end{aligned}$$

The sensitivity of any individual was shown above to be $S = M/\bar{M}$. The sensitivities, S_i and S_j, of any two individuals or populations are related to their respective means by

$$S_i/S_j = M_i/M_j.$$

So if t denotes a selected population and 0 the base population with $S_0 = 1$, the sensitivity after selection will be

$$S_t = M_t/M_0. \tag{10}$$

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