

NOTES AND COMMENTS

SELECTION FOR ASYMMETRICAL BIAS IN A BEHAVIOURAL CHARACTER OF *DROSOPHILA MELANOGASTER*

DAVID J. PURNELL* and JAMES N. THOMPSON, Jr.
*University of Cambridge, Department of Genetics, Milton Road,
Cambridge CB4 1XH*

Received 16.v.73

SUMMARY

Two lines of wild type *Drosophila melanogaster* were selected for asymmetrical bias in the direction in which they folded their wings. Both the Left over Right and the Right over Left selection lines produced significant responses to selection for the first few generations; but, after a 6-10 per cent bias had been achieved, the accumulated response was lost in each line. While the lines were responding, the sexes alternated in high asymmetry values each generation, suggesting that the relevant alleles may have been sex-linked.

1. INTRODUCTION

INHERITED lateral bias in any character is a tendency for asymmetry to be expressed on one particular side of a bilaterally symmetrical organism. Asymmetrical bias is common in nature, not only for morphological traits such as the direction of shell coiling in snails and claw size in crabs, but also for behavioural traits such as handedness in man. Asymmetry has been used as a measure of developmental homeostasis (see Thoday, 1958) and various studies have shown that the level of asymmetry could be modified by artificial selection (Mather, 1953; Thoday, 1958; Reeve, 1960, 1961) and by natural selection or a change in the environment (Beardmore, 1960). Beardmore (1965) successfully selected for left and for right bias in sternopleural chaetae number in *Drosophila melanogaster*, and we were interested to learn whether there was also genetic variability for the expression of bias in a behavioural trait. We have, therefore, attempted to select for bias in the direction of wing folding in a wild stock of *Drosophila melanogaster* in which the frequency of left over right (L/R) and right over left (R/L) wing folding phenotypes was approximately equal.

2. MATERIALS AND METHODS

Selection was carried out using the Eversden-14 wild type stock of *Drosophila melanogaster*, which was derived from a single inseminated female collected near Cambridge, England, in October 1970. Prior to the start of this experiment, the stock had been maintained in mass culture for about 30 generations.

From this mass culture 50 virgin females and 50 males were separated into two groups by the way in which they folded their wings. The direction of wing folding is determined by which wing is drawn in first. Thus, if the

* Present address: Department of Genetics, University College of Swansea, Singleton Park, Swansea, Glamorgan.

left wing is closed first, the right wing will be on top and the direction of wing folding will be recorded as right over left, and vice versa. After 24 hours these two groups of flies were assayed again and from the subgroups of flies that had folded their wings in the same direction for both assays, five flies of each sex were taken at random as parents of the first generation. For each subsequent generation, directional selection was continued within each of the cultures by selecting, from 50 virgin flies of each sex, five pairs from the group that had folded their wings in the required direction for two assays.

From the unselected stock 10 flies of each sex were taken at random and assayed for direction of wing folding on 10 separate occasions. This preliminary assay indicated that, although the population as a whole showed no bias for direction of wing folding, each individual fly did show a strong tendency to close the same wing first each time.

Although the direction of wing folding is behavioural, the effects of selection can perhaps be visualised in terms of anatomical modifications far more easily than for many other behavioural characters. An inherited bias for closing one wing before the other could conceivably be traced to any number of modifications in the muscular or neural organisation of the *Drosophila* wing and thorax.

3. RESULTS AND DISCUSSION

The responses to selection, averaged over both sexes, are illustrated in fig. 1, *a*. For convenience in presentation asymmetrical bias is shown as a deviation from the mean expression of the unselected Eversden-14 wild type stock. An increase in L/R phenotypes is arbitrarily shown as a positive deviation, while an increase in R/L phenotypes is shown as a negative deviation.

An analysis of variance of the joint regression (table 1) for the first four generations of the L/R selection line and the first eight generations of the R/L selection line shows that during the initial responses, the lines diverged significantly. This positive response to selection demonstrates the presence of some genetic variability for the direction of wing folding.

Although the lines responded during the first generations of selection, this response was not maintained. Periods of response were analysed separately in table 2. During the first four generations the expression of the L/R line increased to a 6 per cent. deviation ($b = 1.7$; $P < 0.01$). At generation 5, however, the accumulated response was lost and deviations fluctuated around zero until the experiment was terminated at generation 15. Similarly, the frequency of flies with R/L phenotypes increased in the R/L selection line until an 8-10 per cent. deviation had been attained at generation 8 ($b = 1.3$; $P < 0.01$), after which the response was lost and expression fluctuated randomly until generation 15.

Further information is gained if the male and female means are graphed separately for each line (L/R in fig. 1, *b*; R/L in fig. 1, *c*). The response of each line can be divided into two phases. During the early generations of selection (1-4 in L/R; 1-8 in R/L), the sexes alternated in high asymmetry values each generation. Thereafter, the zig-zag pattern was replaced by seemingly random fluctuations in which both sexes responded together. Thus, the zig-zag alternation in phenotypic means occurred only during the period in which the two lines were responding to selection.

It is difficult to suggest any mechanism causing an inherited asymmetrical bias that does not involve some initial modification of the egg cell or very

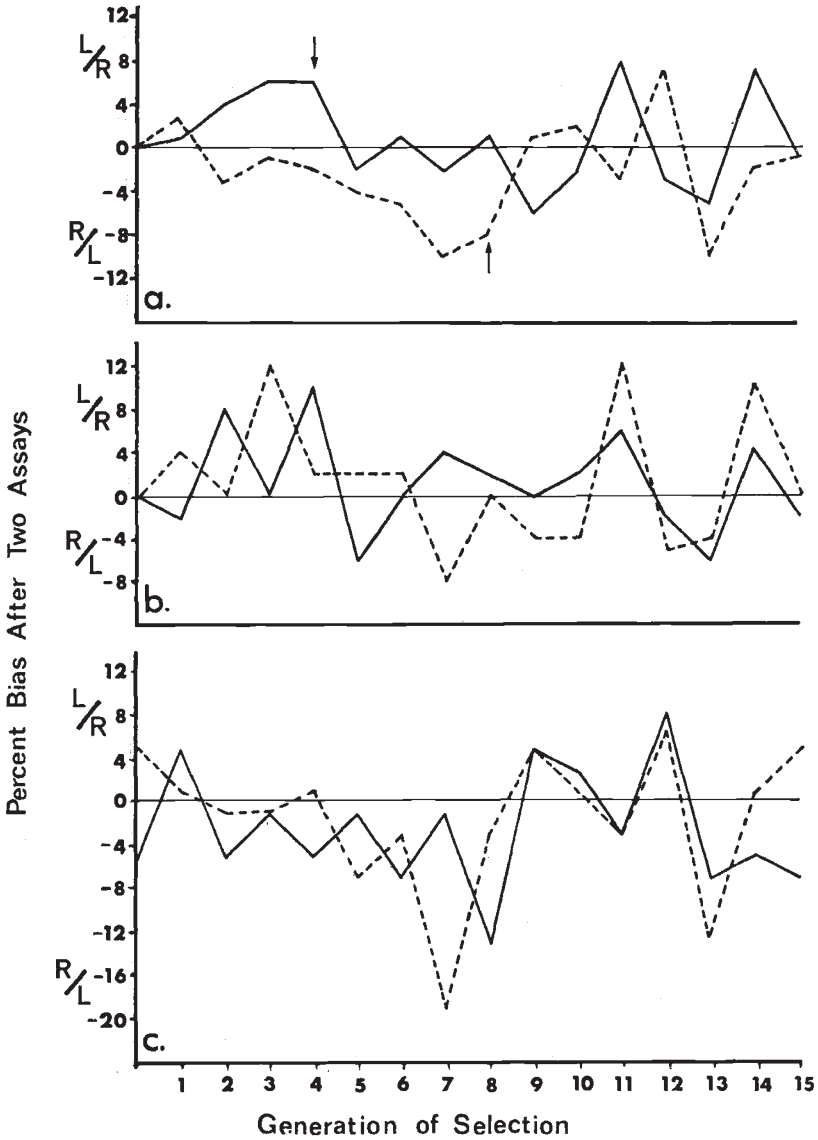


FIG. 1.—Responses to selection for direction of wing folding: (a) Left over Right (solid) and Right over Left (dashed) averaged over sexes; (b) Left over Right selection line females (solid) and males (dashed); (c) Right over Left selection line females (solid) and males (dashed). The arrows in (a) indicate the generations at which the alternating high asymmetry in male and female means was lost.

early cell divisions. Although the initial difference must almost certainly be associated with some event or distribution of substances in the egg cytoplasm, this does not imply that the effects of these changes must be observed

immediately. It is only in the later stages of development that the organism must possess the necessary signals to cause the development of the two sides to differ in a predictable way. The patterns of response in the two lines are,

TABLE 1

Analysis of variance of the joint regression, for L/R generations 0-4 and R/L generations 0-8

Item	d.f.	S.S.	M.S.	<i>t</i>	P
Joint regression	1	46.4143	46.4143	3.7	<0.01
Difference between regressions	1	73.7524	73.7524	4.7	<0.001
Difference between means	1	114.2857	—	—	—
Error	10	33.2556	3.3256	—	—
Total	13	267.7080	—	—	—

therefore, consistent with either of two hypotheses: (1) that selection modified the constituents of the egg cytoplasm, possibly by influencing the distribution of some substance, or (2) that selection exploited genes that had a certain relationship or interaction with the constituents of the cytoplasm. The alternating expression in males and females may indicate that the relevant genes are sex-linked.

TABLE 2

Slope (b) and significance levels of the regression of sections of the selection response curves on generations, when both L/R and R/L biases are represented by positive numbers

Generation of selection	<i>b</i>	<i>r</i> *	d.f.	P
L/R { 0-4	1.700	0.962	3	<0.01
{ 5-15	0.236	0.177	9	n.s.
{ 0-15	-0.178	-0.197	14	n.s.
R/L { 0-8	1.300	0.890	7	<0.01
{ 9-15	0.750	0.311	5	n.s.
{ 0-15	0.062	0.064	14	n.s.

* *r*, Bravais-Pearson coefficient of linear correlation.

The loss of response in both lines is difficult to explain, but may be due to the rather high degree of inbreeding in the selection programme, resulting in the loss of the alleles responsible for the change in phenotype. Alternatively, one might expect there to be limitations upon the amount that symmetry could be tampered with in a selection experiment. For the wing folding character such a limit might have been reached, at least on this genetic background. The loss of accumulated selection response, and presumably the loss of the ability to respond during the second phase, might then be explained as the counter effects of natural selection.

Acknowledgments.—We would like to thank Professor J. M. Thoday and Professor J. A. Beardmore for their helpful discussions and for comments on the manuscript, and Mr C. G. N. Mascie-Taylor for discussing the analysis.

4. REFERENCES

- BEARDMORE, J. A. 1960. Developmental stability in constant and fluctuating temperatures. *Heredity*, 14, 411-422.
- BEARDMORE, J. A. 1965. A genetic basis for lateral bias. Symposium on the mutational process, Prague. *Mutation in Population*, pp. 75-83.

- MATHER, K. 1953. Genetical control of stability in development. *Heredity*, 7, 297-336.
- REEVE, E. C. R. 1960. Some genetic tests on asymmetry of sternopleural chaeta number in *Drosophila*. *Genet. Res.*, 1, 151-172.
- REEVE, E. C. R. 1961. Modifying the sternopleural hair pattern in *Drosophila* by selection. *Genet. Res.*, 2, 158-160.
- THODAY, J. M. 1958. Homeostasis in a selection experiment. *Heredity*, 12, 401-415.

A NOTE ON SOMATIC SEGREGATION OF THE SPECTACLE PATTERN IN POTATOES

N. W. SIMMONDS

Scottish Plant Breeding Station, Pentlandsfield, Roslin, Midlothian

Received 5.vii.73

SUMMARY

The behaviour, over 3-8 generations of vegetative propagation, of nine potato clones showing variable expression of the spectacle pattern is described. Clones differed in expectation of spectacle frequency at equilibrium from 4 to 88 per cent. Variation in spectacle expression depended more upon undefined internal factors than upon environment.

1. INTRODUCTION

THE work reported here is a continuation of studies of variable spectacle patterns on potato tubers described earlier in this journal (Simmonds, 1965). The materials used were the same four cultivated tetraploid (*Andigena* Group) potato clones as before, with the addition of five clones newly selected from *Andigena* seedling populations.

2. RESULTS

(i) *Distribution of spectacle frequencies*

The equilibrium frequency of spectacles (*spt*) in a stock depends upon the frequencies of *spt* tubers among the tubers produced by *spt* (say p) and by non-*spt* (say r): equilibrium, which is independent of initial frequency, is at $r/(1+r-p)$ (Simmonds, 1965). Data for nine clones are summarised in table 1 and show that expected equilibria range very widely from 4 to 88 per cent. In eight cases p exceeds r , generally very widely, but in one clone (63/87) r slightly exceeds p , though presumably only as a freak of sampling. For the clone 62/232 estimates of p , r and equilibrium previously published agree poorly with results in table 1, based on much more extensive observations. The difference is due to sampling and reflects the variability between plants which is characteristic of the material. It was only in the fourth generation that any *spt* tubers were produced at all in the non-*spt* line and the estimate of r was much influenced by the subsequent appearance of relatively few plants with high *spt* frequencies. This behaviour, and the converse, has been noted several times and presumably reflects a change in potentiality for spectacle development early in the life of the young sprout.