

SHORT PAPER

Optimum selection strategies: studies with *Drosophila melanogaster*

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SUMMARY

An experimental evaluation of Jódar & López-Fanjul's (1977) theoretical treatment of the optimum proportions to select when the numbers of males and females scored are unequal has been carried out for sternopleural bristle number in *Drosophila melanogaster*. Three different values of the sex-ratio (c) were considered ($c = 1, 4$ and 10) for the same total number of individuals scored per generation. For each c value two types of line were selected with proportions theoretically maximizing the response to be attained after 10 or 20 generations, respectively. Thus, there were six types of lines and each type was replicated sixfold. A good qualitative agreement was found between the observed and the expected rankings of the different types of selected lines at the designated generations.

1. INTRODUCTION

The infinitesimal model of quantitative inheritance assumes many additive and independent genes of very small effects. Robertson (1970) has shown that under this model the maximum response to t generations of individual selection will be attained if the proportions of selected parents each generation is a function of t/T , where T is the total number of individuals scored per generation. Experimental checks of this theory have been reported by Ruano, Orozco & López-Fanjul (1975) and Frankham (1977). In both cases, good agreement was found between the observed and expected rankings of selection lines with different proportions of selected parents, for values of t/T up to 0.2 ($t = 12-50$, $T = 70-280$), but the concordance was poor for larger values of t/T .

This theory has been extended by Jódar & López-Fanjul (1977) to populations with unequal numbers of males and females scored, showing that the maximum response after t generations of selection is obtained when the number of individuals scored and the optimum proportion selected is the same for males and females every generation. Jódar & López-Fanjul also derived optimum selection strategies when the sex-ratio among scored or selected individuals is not equal to one; these results were confirmed by Cockerham & Burrows (1980) with regard to the procedures for maximizing the limit to selection when the phenotypic distribution of the trait is unimodal and symmetric.

The purpose of the present work is to provide an experimental evaluation of the Jódar & López-Fanjul theory by studying the response achieved by sets of lines of *Drosophila melanogaster* selected with different proportions and sex-ratios.

2. MATERIAL AND METHODS

The design of the experiment is shown in Table 1. From the Aula Dei population, six different types of lines were selected (A_1 , A_2 , B_1 , B_2 , C_1 , C_2), each type replicated six times (denoted by a superscript 1-6). The total number of individuals of both sexes scored in each replicate was 100 per generation. Three values of the sex-ratio among scored

Table 1. *Number of individuals of each sex scored and selected per generation in each replicate*

	Type of line					
	A_1	A_2	B_1	B_2	C_1	C_2
No. scored:						
Males	50	50	20	20	9	9
Females	50	50	80	80	91	91
No. selected:						
Males (m)	5	8	3	6	3	4
Females (f)	5	8	4	7	4	7
Expected effective population size ($4mf/(m+f)$)	10	16	6.9	12.9	6.9	10.2
Expected average intensity of selection	1.65	1.46	1.71	1.43	1.45	1.32

individuals (c) were considered ($c = 1$, types A_1 and A_2 ; $c = 4$, types B_1 and B_2 ; $c = 10$, types C_1 and C_2), the proportions selected of males and females for each type of line being those which would theoretically maximize the response after 10 (types A_1 , B_1 and C_1) or 20 generations (types A_2 , B_2 and C_2). These proportions were obtained from equations (4) and (6) of Jódar & López-Fanjul (1977).

Twenty generations of mass selection were carried out for increased bristle score on the two sternopleural plates according to the procedure shown in Table 1. The number of males and females selected was always as intended, but occasionally the number of scored individuals was lower than required, especially from generation 17. A line was considered to be lost when the number of individuals available was less than that required for selection. All lines were maintained in half-pint bottles at 25 °C and were contemporaneous during the experiment.

3. RESULTS

(i) Response to selection

The three-generation moving average score of females, pooled over replicates and plotted by generation of selection, is shown in Fig. 1 for each type of line. Response to selection was linear in terms of selection differential during the first three generations, in which one-third of the final response occurred. The corresponding realized heritability (0.53 ± 0.03) was not significantly different from the base population estimate (0.61 ± 0.09), obtained by regression of offspring on mid-parent. A smaller rate of response was observed thereafter but some lines were still responding when selection was ended at generation 20.

From generation 10 onwards, considerable losses of lines were experienced by types

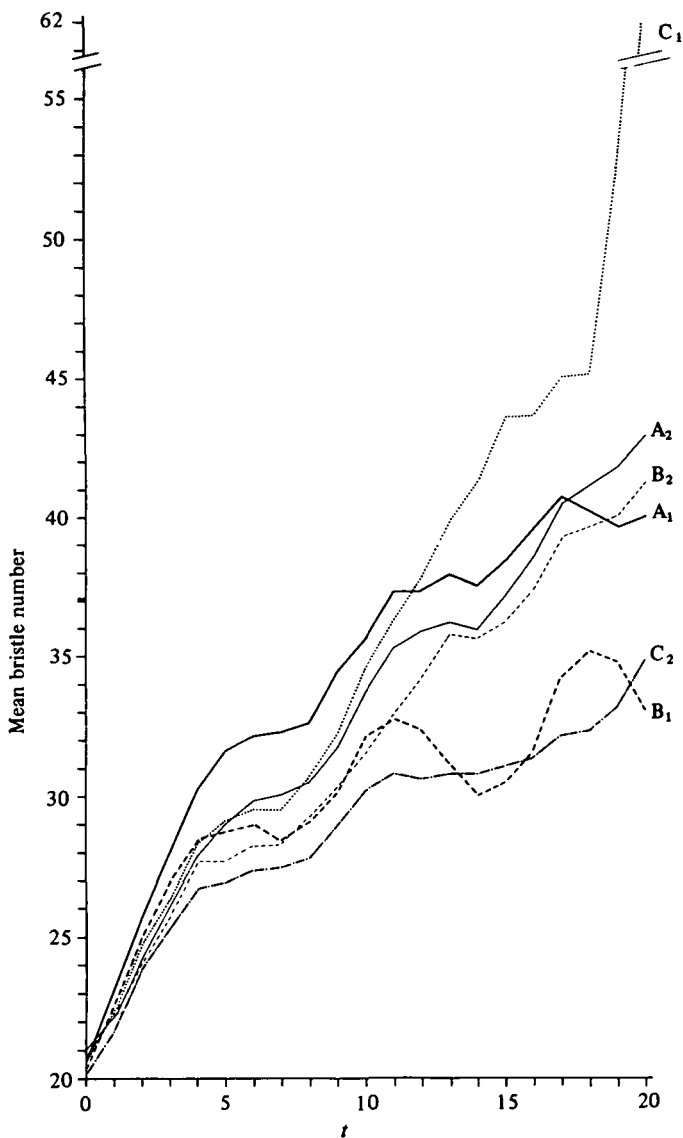


Fig. 1. Scores of the different types of lines pooled over replicates (three-generation moving averages for females)

B₁ and C₁, those with the lowest effective population sizes. These two types were represented by a single replicate at the end of the experiment. On the other hand, 3–4 replicates of the remaining types survived throughout the experiment.

Selection intensities were estimated per line and generation as the applied selection differentials in phenotypic standard deviation units of the corresponding generation. Until generation 15 observed selection intensities pooled over replicates were slightly higher (up to 7%) than expected (Becker, 1975). This could be attributed to departures from normality of the phenotypic distribution of the trait. This distribution, initially moderately skewed to the right, approached symmetry as selection progressed.

(ii) Rankings of the lines at generations 10 and 20

It has been theoretically shown (Jódar & López-Fanjul, 1977) that the maximum response after t generations of selection is obtained when the number of individuals scored and the optimum proportion selected is the same for males and females; the larger the departure from this condition the smaller the expected response. Therefore, predicted rankings of the selected types of lines are $A_1 > B_1 > C_1$ and $A_2 > B_2 > C_2$ at any generation. For an equal value of the sex-ratio among scored individuals we had two types of lines selected with proportions theoretically leading to maximum response after 10 (subscript 1) or 20 (subscript 2) generations, for which predicted rankings are $A_1 > A_2$, $B_1 > B_2$, $C_1 > C_2$ at generation 10 and the reverse ($A_2 > A_1$, $B_2 > B_1$, $C_2 > C_1$) at generation 20.

Analyses of variance failed to show significant differences ($P > 0.05$) between the means of the different types of lines at generation 10 or 20, as a large significant between-replicate divergence was present in both instances. Notwithstanding, the observed rankings were in excellent agreement with the above expectations, excepting some comparisons involving type C_1 ($C_1 > B_1$ at generation 10; $C_1 > C_2$, $C_1 > A_1$, $C_1 > B_1$ at generation 20). It should be noted that type C_1 was represented by a single replicate (C_1^c) at generation 20 and that this line showed a large accelerated response to selection from generation 8 to 22. This response was found to be related to the presence of a recessive lethal associated with the terminal inversion 3R^c.

Considering all six types of lines, their predicted ranking (Jódar & López-Fanjul, 1977) is $A_1 > A_2 > B_1 > B_2 > C_1 > C_2$ at generation 10 and $A_2 > A_1 > B_2 > B_1 > C_2 > C_1$ at generation 20. These specific alternatives can be tested against the null hypothesis ($A_1 = A_2 = B_1 = B_2 = C_1 = C_2$) by the non-parametric method of Jonckheere (1954). The null hypothesis can be rejected in both cases at the 2.5% level.

4. DISCUSSION

This experiment was designed to provide an experimental check of the theory concerning optimal selection strategies after 10 or 20 generations for different pre-fixed values of the sex-ratio among scored individuals (Jódar & López-Fanjul, 1977). A good qualitative agreement was found between the observed and the expected rankings of the different types of selected lines in both instances.

However, there are several factors not considered in the predictions which may nevertheless have affected the results. Effective population sizes may be smaller than their estimates from the number of selected males and females, owing to parents' unequal probability of contributing offspring to the next generation. This can arise both by accidental departures from the model, as we are dealing with mass cultures, and from the practice of artificial selection (Robertson, 1961). Consequently, the between-replicate variance would be larger than expected and a smaller response to selection would be obtained in any generation. Secondly, selection could generate linkage disequilibrium which would in turn reinforce these effects. Nevertheless, the differences in selection intensity and effective population size among types of lines does not seem sufficiently large to alter the relative ranking of the lines, although they are both expected to introduce some noise in the comparisons and also to increase slightly the optimum proportions to be selected (Robertson, 1970).

Fitness clearly declined as selection progressed resulting in considerable losses of lines, particularly those selected with the lowest effective sizes. This could bring about an experimental conflict as the lines more likely to suffer from inbreeding depression would consequently be expected to show a proportionately larger reduction of their intensity of selection in the long-term. This would increase the probability that the performance of lines A_1 , B_1 and C_1 would be respectively surpassed by that of lines A_2 , B_2 and C_2 ,

but for different causes than those considered in the model. However, this progressive reduction of the expected intensity of selection was small, indicating that the departures from the experimental design were unimportant in this respect. Losses of lines also limited the power of resolution of the experiment at the later stages of selection, especially in those comparisons involving types B₁ and C₁, that were each represented by a single replicate at generation 20.

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REFERENCES

- BECKER, W. A. (1975). *Manual of Procedures in Quantitative Genetics*, 3rd ed. Pullman: Washington State University Press.
- COCKERHAM, C. C. & BURROWS, P. M. (1980). Selection limits and strategies. *Proceedings of the National Academy of Science, U.S.A.* **77**, 546–549.
- FRANKHAM, R. (1977). Optimum selection intensities in artificial selection programmes: an experimental evaluation. *Genetical Research* **30**, 115–119.
- JÓDAR, B. & LÓPEZ-FANJUL, C. (1977). Optimum proportions selected with unequal sex numbers. *Theoretical and Applied Genetics* **50**, 57–61.
- JONCKHEERE, A. R. (1954). A distribution-free *k*-sample test against ordered alternatives. *Biometrika* **41**, 133–145.
- ROBERTSON, A. (1961). Inbreeding in artificial selection programmes. *Genetical Research* **2**, 189–194.
- ROBERTSON, A. (1970). Some optimum problems in individual selection. *Theoretical Population Biology* **1**, 120–127.
- RUANO, R. G., OROZCO, F. & LÓPEZ-FANJUL, C. (1975). The effect of different selection intensities on selection response in egg-laying of *Tribolium castaneum*. *Genetical Research*, **25**, 17–27.