# Optimum selection intensities in artificial selection programmes: an experimental evaluation

By R. FRANKHAM*

*Institute of Animal Genetics, West Mains Road, Edinburgh EH9 3JN*

## SUMMARY

An experimental evaluation of Robertson's (1970) theory concerning optimum intensities of selection for selection of varying durations has been carried out using published results from a long term selection study in *Drosophila*. Agreement of predicted rankings of treatments with expectations was excellent for low values of $t/T$ (generations/total number scored) but poor for larger values of $t/T$. This was due to the 20 % selection intensity treatments responding worse than expected and the 40 % treatments relatively better than expected. Several possible reasons for the discrepancies exist but the most likely explanation is considered to be the greater reduction in effective population size due to selection in treatments with more intense selection.

## 1. INTRODUCTION

The optimum design of artificial selection schemes is an important problem in plant and animal breeding. A conflict exists between the designs giving maximum immediate gains and those providing maximum limits to selection. For immediate gains the maximum selection intensity possible provides the maximum selection response, while the highest limit to selection is expected from selecting one half of the population each generation (Robertson, 1960). Smith (1969) and Robertson (1970) have extended the theory to predict the optimum intensity of selection required to obtain maximum selection response after any duration of selection. Robertson (1970) showed that with a constant selection regime the optimum proportion to select ($p$) each generation can be expressed as a function of $t/T$ (generations/total number scored per generation). The optimum values of $p$ are low for small values of $t/T$ and rise in a sigmoid curve to asymptote at an optimum $p$ of 0·5 for large values of $t/T$.

The purpose of this note is to provide an experimental evaluation of Robertson's (1970) theory using the experimental results of Frankham, Jones & Barker (1968*a*) and Jones, Frankham & Barker (1968). One experimental evaluation of this theory is already available (Ruano, Orozco & López-Fanjul, 1975) but the present study extends considerably the range of $t/T$ over which the theory is evaluated.

* Permanent address: School of Biological Sciences, Macquarie University, North Ryde, N.S.W. 2113, Australia.

## 2. MATERIALS AND METHODS

Full details of the experimental methods and the results are given by Frankham *et al.* (1968*a*) and Jones *et al.* (1968). In brief, the data come from an unequally replicated factorial experiment involving selection for increased abdominal bristle number in *Drosophila melanogaster* for 50 generations in selection treatments with a range of population sizes (10, 20 and 40 pairs of parents) and selection intensities (10 %, 20 %, 40 % and controls). Treatment codes are of the form population size (proportion selected), for example 20 (10 %) is the treatment with 20 pairs of parents per generation selected at an intensity of 10 % each generation.

The selection treatments available for evaluating the theory are:
(i)   $T = 400$, treatments 20 (10 %) and 40 (20 %).
(ii)  $T = 200$, treatments 10 (10 %), 20 (20 %) and 40 (40 %).
(iii) $T = 100$, treatments 10 (20 %) and 20 (40 %).

Comparisons with theory were done for selection response at generations 12, 25, 35 and 50.

In Robertson's theory the values of $T$ are the ratio of effective population size ($N_e$) and proportion selected ($p$). The above values of $T$ have been computed using the actual populations sizes ($N$) so they require adjustment to reflect the effective population size. The values of $T$ in Table 1 were obtained by multiplying those above by 0·7 in an attempt to adjust for this effect. This value of 0·7 for $N_e/N$, the ratio of effective to actual population size is based on Crow & Morton (1955).

Theoretical optimum proportions to select for each $t/T$ combination were obtained by finding arithmetically the value of $p$ maximizing selection response in Robertson's (1970) unnumbered equation

$$\Delta G^{(t)} = \frac{2TzV_A}{\sigma}\left(1 - e^{-t/2Tp}\right)$$

where $\Delta G^{(t)}$ is the response after $t$ generations of selection, $\sigma$ the phenotypic standard deviation, $z$ the ordinate of the normal distribution at the point of truncation when the area cut off is $p$, and $V_A$ is the additive genetic variation.

The optimum values of $p$ were checked against values read off Robertson's Fig. 1.

## 3. RESULTS AND DISCUSSION

The response to selection for each of the selection treatments is presented in Fig. 1 with the generations at which comparisons were made indicated by vertical lines. The figures plotted are the means of scores for males and females and they are plotted every five generations, with the addition of generation 12. The means of the controls over the same period are also presented. The values of $t/T$, the corresponding theoretical optimum values of $p$ and the observed rankings of the selection treatments are presented in Table 1.

The observed rankings of treatments are in excellent agreement with the predicted optima up to a $t/T$ of approximately 0·18, there being only one comparison disagreeing with expectations in this range. Ruano *et al.* (1975) also

found agreement with expectations in this range. However, above this value of $t/T$ the agreement with expectations is rather poor, none of the comparisons showing the expected rankings of treatments. This is due to the 20 % treatments responding less than expected and the 40 % treatments better than expected.
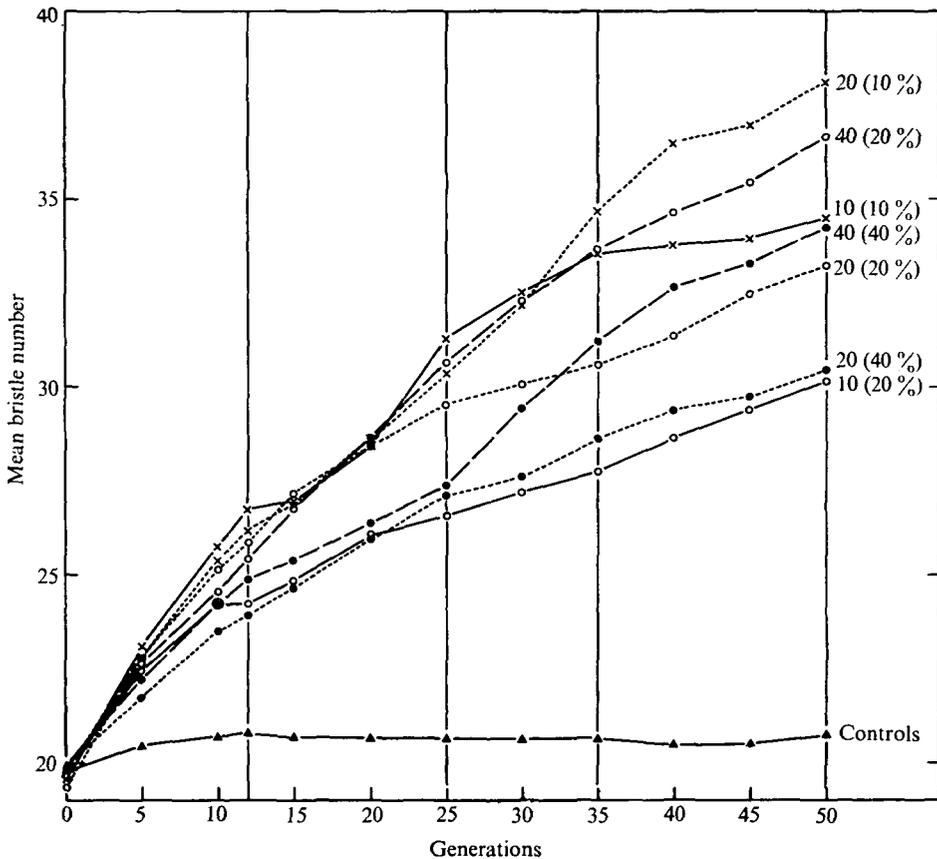


Fig. 1. Response to selection (treatment means).

This discrepancy between observed and predicted rankings for higher values of $t/T$ could be due to (i) chance, (ii) assumptions underlying the theory not being met, or (iii) the ratio of effective to actual population size being less than assumed.

The sampling variance about the means increases with generations so comparisons in later generations are less reliable than those in earlier generations. All discrepancies are found after 25 or more generations of selection. It should also be noted that the variation among replicate lines within the selection treatments was large and a number of lines showed irregular patterns of selection response (Jones *et al.* 1968), so the sampling variation about the treatment means is large.

The effects of linkage are ignored in Robertson's theory but he showed that linkage is expected to increase slightly the optimum proportions to select (Robertson, 1970). This could at least partly account for the discrepancies, as linkage

effects are likely to be important in *Drosophila melanogaster* with its four pairs of chromosomes and absence of crossing over in males. The second assumption of the theory which might be violated is that changes in the genetic variation due to selection can be ignored, *i.e.* genes of large effect are not making an important contribution to the genetic variation. If genes of large effect are making an important contribution to the genetic variation then the genetic variation will

Table 1. *Predicted optimum selection intensity and observed rankings of selection treatments for various values of* t/T

| Generations/Total size (t/T) | Predicted optimum p (%) | Observed ranking |
|---|---|---|
| 12/280 = 0·043 | 5 | 20 (10 %) > 40 (20 %) |
| 12/140 = 0·086 | 8 | 10 (10 %) > 20 (20 %) > 40 (40 %) |
| 25/280 = 0·089 | 8 | 40 (20 %) > 20 (10 %) |
| 35/280 = 0·125 | 10 | 20 (10 %) > 40 (20 %) |
| 12/70 = 0·171 | 12 | 10 (20 %) > 20 (40 %) |
| 25/140 = 0·179 | 13 | 10 (10 %) > 20 (20 %) > 40 (40 %) |
| 50/280 = 0·179 | 13 | 20 (10 %) > 40 (20 %) |
| 35/140 = 0·250 | 16 | 10 (10 %) > 40 (40 %) > 20 (20 %) |
| 25/70 = 0·357 | 19 | 20 (40 %) > 10 (20 %) |
| 50/140 = 0·357 | 19 | 10 (10 %) > 40 (40 %) > 20 (20 %) |
| 35/70 = 0·500 | 23 | 20 (40 %) > 10 (20 %) |
| 50/70 = 0·714 | 28 | 20 (40 %) > 10 (20 %) |

decline more rapidly than expected and the optimum proportions to select will be higher than predicted. There are grounds for suspecting that genes of large effect are contributing to the genetic variation for this character. A substantial proportion of the selection lines had recessive lethal genes which reached high frequencies, and some of these behaved as if they had large pleiotropic effects on abdominal bristle number (high variances, large regression on relaxation and a large response to reverse selection) (Frankham, Jones & Barker, 1968*b*). Davies (1971) has presented evidence that genes of large effect make important contributions to selection reponse for this character. His evidence, however, must be evaluated carefully in the light of MacMillan & Robertson's (1974) critical evaluation of his experimental technique.

If the ratio of $N_e/N$ is less than the value of 0·7 assumed, the predicted optimum values of $p$ would be increased above the values given in Table 1 as the values of $t/T$ would be increased. The ratio of effective to actual population size used probably represents an upper limit in the range of likely values, as it derives from populations not being subjected to artificial selection (for which no values of $N_e/N$ are available). Artificial selection is expected to lower the value of $N_e/N$ (Robertson, 1961), the expected values of $N_e/N$ for the 10 %, 20 % and 40 % treatments being approximately 0·45, 0·65 and 0·79. Clearly this effect will both reduce the effective size of the selection units and also reduce it more in the higher selection intensity treatments. For this reason the rate of decline in genetic variation will be highest with the highest intensity of selection and lowest with the lowest intensity of selection in a manner which would largely explain the observed

discrepancies. This effect would seem to be the most likely one to explain the rather better than expected performance of the lowest selection intensity treatments. It would, however, have been expected to affect the 10 % selection intensity treatments most of all, but these didn't respond poorly. It would be worthwhile to extend the theory to include this inbreeding effect of selection.

In conclusion, the agreement between observed and expected rankings of selection treatments is not particularly close, especially for higher values of $t/T$. The discrepancies could be due to chance, to a lower ratio of $N_e/N$ than that assumed, to the effects of linkage, to genes of large effect or to the greater reduction in effective population size due to selection with greater intensities of selection. All of these factors may be contributing but the last may be the most important reason for the discrepancies.

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