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The effects of population size and selection intensity in selection for a quantitative character in *Drosophila*

I. Short-term response to selection

By R. FRANKHAM*, L. P. JONES† and J.S. F. BARKER
Department of Animal Husbandry, University of Sydney, Sydney, N.S.W., 2006, *Australia*

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1. INTRODUCTION

Although a number of workers (Lerner & Hazel, 1947; Clayton, Morris & Robertson, 1957; Martin & Bell, 1960) have reported fair agreement between observed selection responses and those expected from base population estimates of heritability, there is little information on the effect of population size and selection intensity on selection response and on realized heritability.

Clayton *et al.* (1957) found that realized heritability decreased as selection intensity decreased, but suggested that this needed to be checked with further experiments as the agreement between replicate lines was generally poor.

The effect of population size on realized heritability has not been measured, but a comparison of the responses obtained in inbred lines and in outbred lines suggests that population size could have an appreciable effect even within a few generations. In selection for wing length in *Drosophila melanogaster*, Tantawy (1956) obtained less response under a double first-cousin mating system than under outbreeding, and even less response under sib-mating. In selection experiments for high and low responses to gonadotrophic hormone in rats, Chung & Chapman (1958) obtained less response than expected under an 'inbred' mating scheme; while under their 'outbred' and 'crossbred' mating schemes, responses were equal to or greater than predicted. Similarly, Lewis & Warwick (1953) found a lower realized heritability in selection for body size in mice under inbreeding than under outbreeding.

In the experiments described here, the effects of population size and selection intensity on the short-term response to artificial selection and the precision of heritability predictions were investigated.

2. MATERIALS AND METHODS

The Canberra strain of *D. melanogaster* described by Latter (1964) was used. Since March 1964 (about 3 months prior to initiation of this experiment), it has been maintained in our laboratory as a cage population averaging about 3000–4000 adults.

Present addresses: * Canada Department of Agriculture Research Station, Lacombe, Alberta, Canada. † Department of Genetics, University of Minnesota, St Paul, Minnesota, U.S.A.

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The character selected was the number of bristles on one abdominal sternite—fourth in males and fifth in females. In the Canberra-base population at the first generation scored (generation 0), the mean and standard deviation were $21{\cdot}7 \pm 2{\cdot}02$ in females and $17{\cdot}7 \pm 1{\cdot}93$ in males.

The experiment was set up as an unequally replicated factorial design of three population sizes (10, 20 and 40 pairs of parents) and five selection intensities (10, 20, 40, 80 and 100% (unselected controls)), with one to five replicates (Table 1). Replication was limited by the time involved in scoring any particular line, and for the larger populations because the effect of chance was expected to be less.

Table 1. *Experimental design, treatment code designation, number of replicates per treatment* (n) *and total number of pairs scored each generation in each replicate* (T)

Population size (pairs of parents)		Selection intensity				
		10%	20%	40%	80%	Controls
10	Code	10(10%)*	10(20%)	10(40%)	10(80%)	10(C)
	n	4	5	5	5	5
	T	100	50	25	12 or 13	20
20	Code	20(10%)	20(20%)	20(40%)	20(80%)	20(C)
	n	2	3	3	3	3
	T	200	100	50	25	20
40	Code	40(10%)	40(20%)	40(40%)	40(80%)	40(C)
	n	1	2	2	2	2
	T	400	200	100	50	40

* Replicate lines within treatments are referred to as, for example, 10(10%)a, 10(10%)b, 10(10%)c and 10(10%)d.

An egg sample was taken from the cage population and the strain maintained for three generations, using sixteen bottles (5 oz. cream jars) per generation and the maintenance procedure used throughout the selection programme, that is, five pairs of parents per bottle on a dead yeast fortified medium (medium F of Claringbold & Barker, 1961) at $25 \pm 0{\cdot}5$ °C and 65–70% relative humidity.

Each line was commenced with a sample of virgin flies, equal in number to the population size of the line and chosen more or less equally from the sixteen bottles of the third generation. Controls and 80% selection lines were set up so that pairs of lines originated from the same parents, e.g. 20(80%)c and 20(C)c were commenced with the same 20 pairs of flies, whose progeny were split into two samples to score generation 0.

In the following generation (designated generation 0), mass selection was commenced on a within-bottle basis. The five females and five males with the highest bristle number were selected from the appropriate number of virgin flies. For the 10 and 20% lines, 50 and 25 pairs of flies per bottle were scored. For the 40% lines, 13 females and 12 males were scored from one bottle and 12 females and 13 males from the next. Similarly, for the 80% lines either 12 or 13 were scored per bottle. The randomly chosen parents were scored in the control lines. With 10(80%) and

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10(C) the procedure for selecting parents was similar to that of comparable treatments. However, after the parents of the next generation were selected, extra flies were scored so that the mean was estimated from 20 pairs for each of these lines. The flies selected from the various cultures within each line were bulked, and then randomly assigned in lots of five pairs to new bottles to produce the next generation.

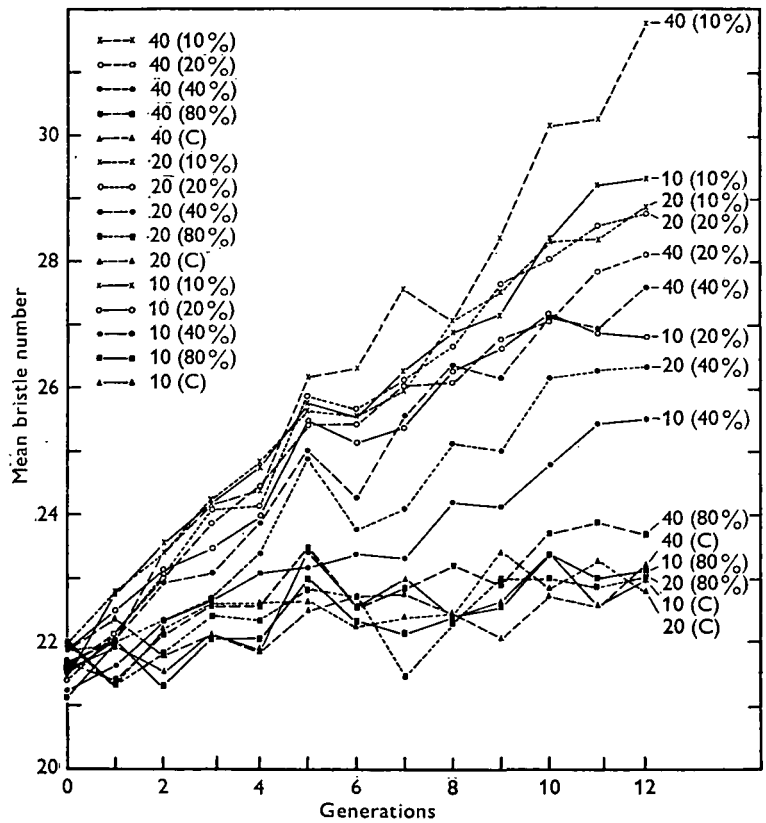

Fig. 1. Response to selection (treatment means).

3. RESULTS

(i) *Response to selection*

The results for the first 12 generations of selection are presented in this paper. Subsequent results are presented in a later paper (Jones, Frankham & Barker, 1968). Mean abdominal bristle number of the females each generation is shown for the various treatments in Fig. 1. Males showed a similar proportional response and have not been included. There was considerable response to selection for all selection treatments except the 80%. As expected, higher selection intensities produced more response for the same population size, i.e. in response 10(10%) > 10(20%) > 10(40%) > 10(80%), and similarly for the 20- and 40-pair treatments.

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For the same selection intensity, the effect of population size was not so clear. There was, however, a trend for the larger population sizes to give more response to selection, i.e. in response 40(10%) > 20(10%) and 10(10%), 40(20%) and 20(20%) > 10(20%), 40(40%) > 20(40%) > 10(40%), and 40(80%) > 20(80%) and 10(80%). Even at this early stage 40(40%) had already overtaken 10(20%).

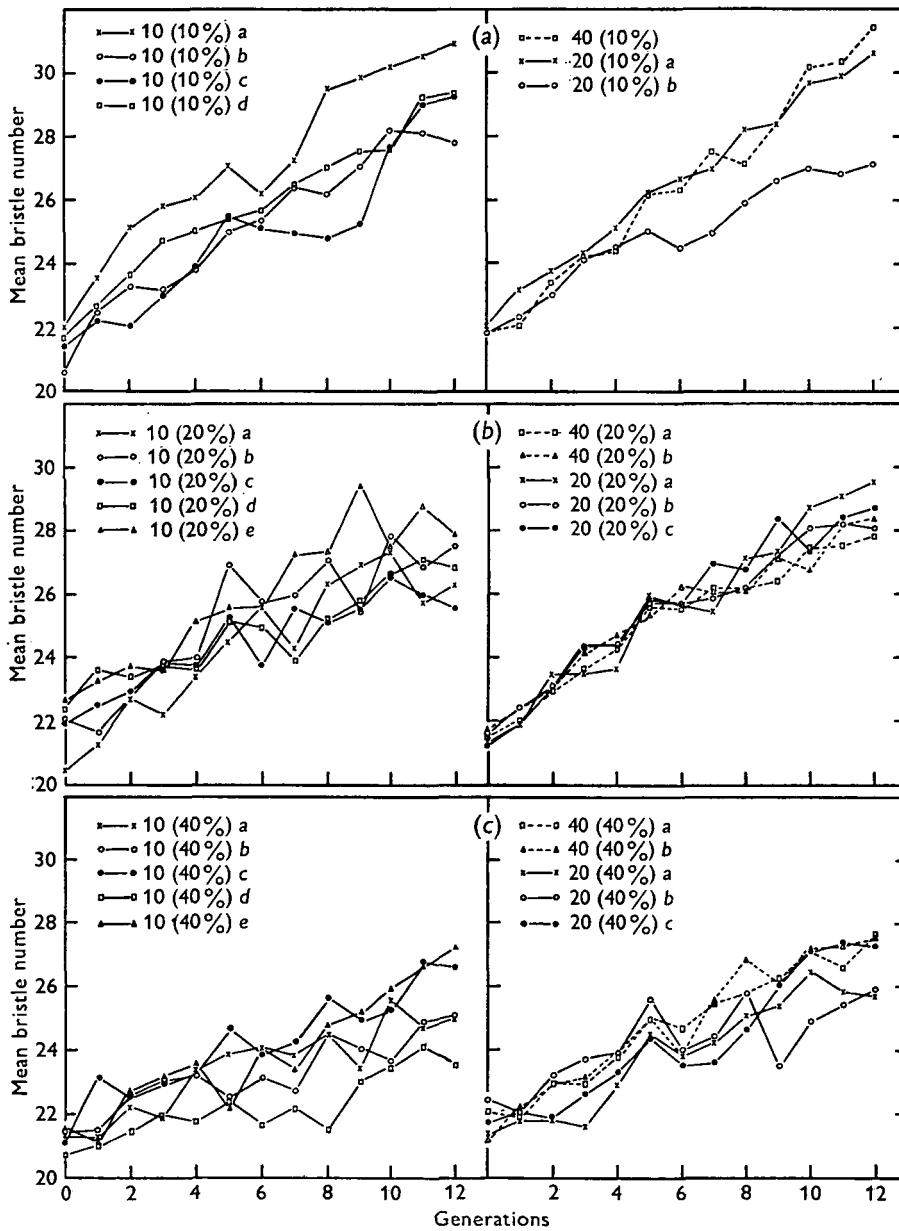

Fig. 2. Response to selection of individual lines. (*a*) 10% lines; (*b*) 20% lines; (*c*) 40% lines.

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Response in the 80% treatments was small and as all controls rose during the first few generations, it is difficult to decide whether or not the response of the 80% treatments was real.

Figure 2*a* shows the response of the 10% lines. Large differences between replicates are evident for 10(10%) and 20(10%). The response of 20(10%)b was poor in comparison with 20(10%)a and the 10(10%) lines, and thus at generation 12 the 20(10%) treatment mean was a little less than 10(10%) and not different from 20(20%).

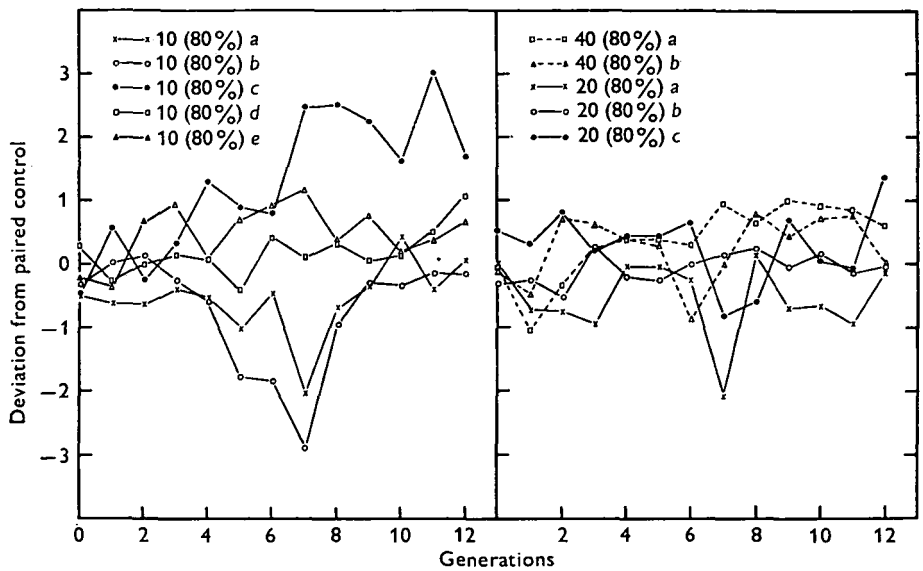

Fig. 3. Mean of male and female deviations of individual 80% lines from paired controls.

Again with the 20% lines (Fig. 2*b*), there were large differences between replicates of the 10-pair treatment. Differences between 40(20%) and 20(20%) were only small, but the superiority of these over the 10(20%) was quite consistent. There were also large differences between replicates of the 10-pair treatment for 40% selection intensity while the 40-pair replicates showed excellent agreement (Fig. 2*c*). The 40(40%) lines were consistently better than the 20(40%) and 10(40%) lines. Two replicates of the latter (10(40%)c, 10(40%)e) gave equal or better response than the 20(40%) lines, while 10(40%)d showed very poor response.

As the responses in the 80% lines were very small, these have been plotted as the mean of male and female deviations from the paired control line, i.e. 10(80%)e was plotted as a deviation from 10(C)e, 20(80%)b as a deviation from 20(C)b, etc. (Fig. 3). Marked differences between replicates were present and violent generation to generation fluctuations are evident. Over-all, there was a small response in the 80% lines but this was less than the approximately one bristle response expected.

Figure 4 shows the female means for the controls over the 12 generations. Large generation to generation fluctuations were present and there was considerable

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divergence between lines. As for the other treatments divergence between replicates decreased as population sizes increased. The controls rose by about one bristle over the first five generations and remained relatively constant thereafter. Of the individual lines 10(C)c and 20(C)a fell slightly while the remainder rose. Possible reasons for the initial rise in the controls were discussed by Rathie (1967). The most likely reason is that the environments of generations 0 to 2, on the average, reduced bristle number. The increase in bristle number at generation 5 and fall at generation 6 in many of the lines supports this suggestion.

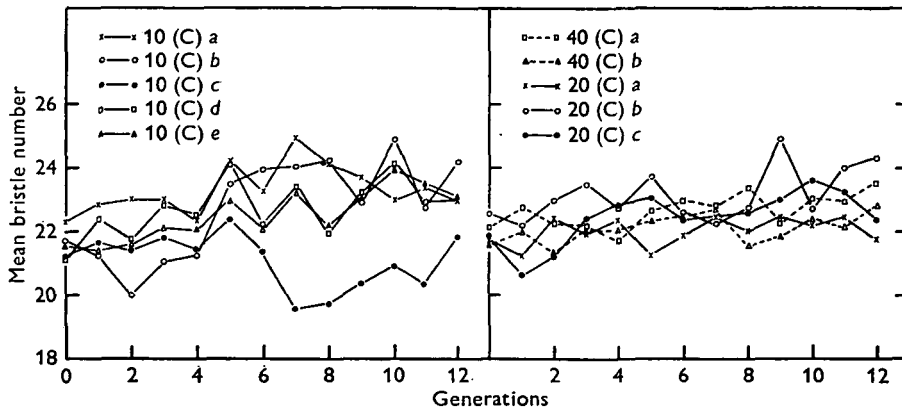

Fig. 4. Mean bristle number of individual controls.

(ii) *Selection differentials*

The average selection differential for each of the selection lines over the first 12 generations is shown in Table 2, together with the expected value. This latter was calculated by multiplying the standardised selection differential for intensities of 5/50, 5/25, etc. (from Falconer (1960) and Becker (1964)), by the average standard deviation for the base population. There was considerable variation between replicate lines, and values tended to be less than expected, this tendency being least for the 10% lines.

(iii) *Heritability*

From the proportions of additive autosomal and sex-linked variation in the base population, Sheridan *et al.* (1968) suggested that the response to selection could be predicted using a heritability of 0·15.

The realized heritability for each line obtained from the regression of response to selection on cumulative selection differential is shown in Table 3. Response to selection was calculated as a deviation from the weighted mean of the controls for the 10, 20 and 40% lines, and as a deviation from the paired control line for the 80% lines. There was considerable variation between replicate lines in their realized heritabilities, this being extremely large for the 80% treatments and also large for 10(20%), 10(40%), 20(10%) and 20(40%). The 10(10%), 20(20%),

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40(20 %) and 40(40 %) treatments all showed good agreement between replicates. Except for 20(10 %), the agreement between replicates for realized heritability tended to be better as the number of individuals scored per line increased.

Table 2. *Average selection differential* (i) *for each line and treatment combination, together with expected values*

Line	*i*	Line	*i*	Line	*i*	Line	*i*
10(10 %)a	3·37	10(20 %)a	2·44	10(40 %)a	1·54	10(80 %)a	0·41
b	3·33	b	2·53	b	1·56	b	0·52
c	3·16	c	2·44	c	1·52	c	0·48
d	3·01	d	2·34	d	1·50	d	0·55
		e	2·47	e	1·57	e	0·60
Average	3·22		2·44		1·54		0·51
20(10 %)a	3·36	20(20 %)a	2·59	20(40 %)a	1·70	20(80 %)a	0·60
b	3·05	b	2·46	b	1·61	b	0·58
		c	2·55	c	1·70	c	0·52
Average	3·20		2·53		1·67		0·57
40(10 %)	3·40	40(20 %)a	2·45	40(40 %)a	1·70	40(80 %)a	0·52
		b	2·52	b	1·72	b	0·52
Average	3·40		2·48		1·71		0·52
Expected 10 %	3·36	20 %	2·67	40 %	1·79	80 %	0·58

Table 3. *Realized heritability* (%) *for each line*

Line	h^2	Line	h^2	Line	h^2	Line	h^2
10(10 %)a	17·16	10(20 %)a	14·65	10(40 %)a	14·63	10(80 %)a	9·70*
b	14·44	b	12·89	b	11·44	b	0·25*
c	15·38	c	7·89	c	16·99	c	46·45
d	14·95	d	11·74	d	11·27	d	10·36*
		e	18·12	e	21·82	e	8·81*
20(10 %)a	16·23	20(20 %)a	19·80	20(40 %)a	18·01	20(80 %)a	−2·74*
b	10·63	b	16·20	b	9·84	b	5·28*
		c	17·96	c	23·45	c	0·87*
40(10 %)	18·72	40(20 %)a	15·80	40(40 %)a	19·91	40(80 %)a	23·04
		b	15·87	b	20·72	b	7·10*

* Not significantly different from zero

Table 4. *Mean realized heritability* (%) *for each treatment*

Population size (pairs of parents)	Selection intensity 10 %	20 %	40 %	Mean*	80 %
10	15·48	13·06	15·23	14·59	15·11
20	13·43	17·99	17·10	16·17	1·14
40	18·72	15·84	20·32	18·29	15·07
Mean	15·88	15·63	17·55	16·35	10·44

* Excluding 80 % treatments

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Table 4 shows the mean realized heritability for each treatment. First, there was a trend for increased realized heritability with increased population size. Taking the means over all selection intensities (except 80%), the realized heritabilities were 14·6, 16·2 and 18·3% for 10-, 20- and 40-pair treatments respectively. Secondly, for units with the same number scored (10(20%) and 20(40%); 10(10%), 20(20%) and 40(40%); 20(10%) and 40(20%)), the realized heritability increased as selection intensity decreased. The mean of 16·4% over all treatments (except 80%) was slightly higher than the predicted heritability (15%). For the same population size, there was no consistent effect of selection intensity on realized heritability. With 80% selection the realized heritability was of a similar magnitude to the other treatments for 10(80%) and 40(80%), while the value for 20(80%) was considerably lower. However, the amount of selection applied was small (cumulative selection differential about 6 bristles over 12 generations), and it is impossible to draw definite conclusions concerning the effectiveness of 80% selection.

4. DISCUSSION

The average realized heritability (16·4%) over all treatments except 80% was slightly greater than that (15%) estimated from the base population. As the latter had large sampling errors (Sheridan *et al.* 1968), this difference is non-significant. As the average population size (pairs of parents) used in these lines was large in relation to many previous laboratory selection experiments, one might imagine that this agreement between realized heritability and the base population estimate would allow reasonable faith to be placed in heritability predictions, at least in the short term. However, responses of individual lines often diverged markedly from their predicted response, with replicate lines differing widely in realized heritability and to a lesser extent in average selection differentials. For example, the response of line 20(10%)a agrees almost perfectly with prediction, while its replicate (20(10%)b) showed much lower response due to a low realized heritability and reduced selection differential.

Sheridan *et al.* (1968) suggested that an appreciable portion (18%) of the variance for one abdominal segment in the Canberra base population was additive × additive epistatic. Griffing (1960) showed that this variance would contribute to the selection response but that its contribution would soon approach a limit unless linkage was very tight. Thus the additive genetic variance should underestimate the response in the early generations when epistasis is present. But as the contribution from epistasis soon approaches a limit, a curvilinear pattern of response is expected. A similar pattern is also expected if additive genetic variance declines or if natural selection opposes artificial selection. A curvilinear pattern of response occurred in a few treatments (e.g. 10(20%) and 20(40%)), but in others (e.g. 10(40%) and 40(10%)) the response was linear. Griffing's (1960) model assumed that population size was infinite and that effects of genes were small. When these conditions are not met the accuracy of his predictions is lowered and errors accumulate as the population mean moves from its initial value. Consequently, his

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predictions are likely to be valid for only a few generations. Depending on the initial gene frequencies, the proportions of additive and epistatic variance may either increase or decrease with time, so it is not clear from the response patterns whether epistasis has contributed to the responses. Griffing (1960) also showed that on relaxation of selection, a similar decline is expected if either epistasis is present or natural selection opposes artificial selection. For about half of the selection lines, relaxed lines split off at generations 5 and 10 fell from one to two bristles after five generations of relaxation (Frankham, Jones & Barker, 1968). It is likely then that epistasis made some contribution to the response, but its effects would be difficult to distinguish from those of natural selection unless one had large numbers of replicate selection lines and far more precise estimates of variance components than we have obtained.

Clayton *et al.* (1957) found fairly good agreement between the average response obtained during seven generations of selection for increased bristle number on two abdominal segments of *Drosophila melanogaster*, and that predicted from base population parameters, but they also had poor agreement between replicates. Agreement with prediction was best at their highest selection intensity (20%) and became worse as selection intensity decreased. In our lines there was no consistent effect of selection intensity on realized heritability. However, in both their experiment and ours, 80% selection was not very effective, although the expected responses were quite small, and agreement between replicates was poor. We therefore cannot make definite conclusions about low selection intensities, except to suggest that they are unlikely to be very effective. Clayton *et al.* (1957) also selected for decreased bristle number but the responses were much less than expected, apparently due to a very rapid decline in genetic variance.

Sheldon (1963) obtained only half the predicted response over ten generations in high lines selected for the same character as Clayton *et al.* (1957), but his low lines responded more than expected. Agreement between his two replicates was good in both directions for short-term responses. He pointed out that when asymmetrical selection response is obtained, heritability predictions only predict divergence between high and low lines.

Latter (1964), using the same Canberra strain as we used, selected for seven generations for the sum of bristle number on two sternites at an intensity of 50/100 pairs in each of two replicates in both directions. He obtained good agreement between replicates, but the equivalent realized heritability for one sternite bristle number of 29·1% was higher than in our most similar treatment (40(40%)). This may have been due to culture conditions as he used a medium with only about a third of the dead yeast that we used. Alternatively, the genetic variance of the base population may have declined since his study, but the large number of parents used to maintain the population makes this unlikely.

Martin & Bell (1960) selected for body weight in *Drosophila melanogaster* and obtained realized heritabilities which were slightly less than the base population heritability. Agreement between the two replicates in either direction was poor, but the divergence between high and low lines in the two experiments was similar.

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Good agreement between observed responses and those predicted from estimates of genetic parameters in the base population or in the early generations of selection have been obtained with other species (Lerner & Hazel, 1947; Hetzer, 1954; Hetzer, Zeller & Hine, 1958; Chung & Chapman, 1958; Enfield, Comstock & Braskerud, 1966). Hetzer (1954) obtained poor agreement between three replicates in selection for black-spotting in swine, while Chung & Chapman (1958) obtained poorer agreement with inbred than with outbred lines of rats. Enfield *et al.* (1966) obtained good agreement between two replicates of *Tribolium castaneum* selected for increased pupa weight. Chance effects would have been less important in their lines than in those of other workers as they used large populations (36 males and 72 females).

Our results show that even for short-term response to selection large population sizes tend to give greater response. This was most clearly indicated by 40(40%) which had already overtaken 10(20%). Because of the within-bottle selection used, observed effects of population size on responses would be reduced as compared with selection at the same intensity from the total population, due to reduction in selection differential and possibly also in realized heritability. Thus, it is clear on the basis of our results and those of Lewis & Warwick (1953), Tantawy (1956), and Chung & Chapman (1958) that the effects of population size cannot be ignored even in short-term selection studies. As Gill (1965) found lower responses for smaller populations in a simulation study using an additive model, the differences were probably due to different levels of genetic variation, and should show up as differences in realized heritability between population sizes. In fact, the average realized heritabilities were 14·6, 16·2 and 18·3% respectively for the 10-, 20- and 40-pair lines. In the case of the 40% lines an increase in selection differential from 10(40%) to 20(40%) to 40(40%) also contributed to the increased response, but for the other selection intensities selection differentials were similar for all population sizes. Average selection differentials varied between replicate lines, and were generally less than expected as the variance declined slightly in most lines (see Jones *et al.* 1968 for details).

There was a consistent trend for realized heritabilities to decrease as the selection intensity increased, when comparing populations with the same number of individuals scored, viz. 40(40%) > 20(20%) > 10(10%), 20(40%) > 10(20%), 40(20%) > 20(10%) in realized heritability. Thus, even at this stage, there was an indication that selection intensities nearer to 50% would allow response to continue for longer, and thus perhaps give a greater total response than higher selection intensities, as suggested by Dempster (1955).

As each line was commenced with a sample of flies equal in number to the population size of the line, initial sampling would have been more important for the smaller population sizes. Robertson (1966) found that restriction of the initial sample from 25 pairs to one pair reduced the limits to selection by only about 30%. Therefore, it was unlikely that a restriction of the initial sample from 40 to 10 pairs would have lowered the response much in the early generations, but it could have increased the variation between replicates for the smaller population sizes.

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Because of the large differences between replicates, particularly for smaller populations, estimates of genetic parameters are expected to predict only the average response of a number of lines. The behaviour of individual lines is largely unpredictable. However, as population size was increased, agreement between predicted and observed responses for individual lines tended to improve.

5. SUMMARY

1. The response to selection for increased number of bristles on one abdominal segment was studied over 12 generations using a factorial design of three population sizes (10, 20 and 40 pairs of parents) and five selection intensities (10, 20, 40, 80% and controls).

2. The responses on the average agreed well with those expected from the estimated base population heritability, but individual replicates diverged considerably.

3. Larger populations tended to give greater response to selection, due mainly to larger realized heritabilities.

4. There was no consistent effect of selection intensity on realized heritability.

5. For populations with the same number of individuals scored, less intense selection gave greater realized heritabilities.

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