SELECTION FOR HIGH AND LOW FATNESS IN SWINE

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FOR many years, body conformation and type were the only important criteria available to breeders attempting to improve carcass merit in swine. Although selection based on these criteria was fairly successful, progressive breeders recognized that more accurate measures were needed for continued improvement. In recent years several methods have been developed for measuring backfat thickness and loin eye area in the live hog. The effectiveness of improving carcass quality by selecting for a quantitative trait such as backfat thickness depends on both the heritability of the trait and its genetic correlation with carcass merit. Estimates of these genetic parameters should therefore be of special interest.

Several controlled selection experiments with swine have been reported. Krider *et al.* (1946) studied the effects of selection for rapid and slow growth rate in Hampshires and Dickerson and Grimes (1947) reported on results from selection for high and low feed utilization in Durocs. More recently, Dillard *et al.* (1962) and Gray *et al.* (1965) reported on the effects of selecting for thinner backfat in crossbred and in Poland China swine, respectively.

The purpose of the present paper is to present the results of selecting for high fatness in one line and for low fatness in another line of both Duroc and Yorkshire swine during 10 and 8 generations, respectively. Earlier phases of the work were reported by Hetzer *et al.* (1963). Throughout the experiment, data were collected on reproductive performance, pig viability, rate of growth, feed requirements, body dimensions and various carcass measurements. Results of the correlated responses shown by these traits will be presented in a later paper.

Materials and Methods

The foundation populations consisted of 34 boars and 48 gilts of the Duroc breed and 52 boars and 61 gilts of the Yorkshire breed. The two groups of pigs were weaned from 16 and 23 litters born in the fall of 1954 and in the fall of 1956, respectively. Sixty-two of the Duroc pigs and 48 of the Yorkshire pigs were born at Beltsville while the remainder were purchased as weanlings. The fattest one or two pigs from 15 of the Duroc litters and from 17 of the Yorkshire litters were used as foundation animals of the high-fat lines (D–H, Y–H). Similarly, the one or two leanest pigs in each of the same litters were selected for the low-fat lines (D–L, Y–L). In addition, an unselected control line was formed in each breed (D–C, Y–C) by saving a like number of pigs from the same litters, and randomly choosing one or two pigs from a litter as parents of each successive generation. In the selected lines, selection of parents was based entirely on a pig's own phenotype without regard to its litter classification or record of sibs. Another set of Yorkshire lines was started in 1954 but because of a rather high incidence of hermaphroditism, cryptorchidism, and atresia ani in 1955 these lines were discarded and are not considered in this paper.

Fatness was measured by a pig's average backfat thickness at a liveweight of about 79.4 kg., the range being from 77.1 to 82.6 kg. Backfat probes at this weight had earlier been found to be as accurate for predicting carcass value as probes at heavier weights (Hetzer *et al.*, 1956). All pigs born in 1954 and 1955 were probed at three sites over the back on one side of the body with a metal rule as described by Hazel and Kline (1952). Beginning with pigs born in 1956, the probing was done on both sides of the body with a lean meter as described by Andrews and Whaley (1955). Although metal rule and lean meter probes were found to be rather closely correlated ($r=0.72$), the latter averaged 0.5 cm. higher and the mean difference was highly significant. All metal rule readings were, therefore, increased by 0.5 cm.

Generally 6 boars and 12 gilts were used

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as parents of each generation in the selected lines, and 12 boars and 12 gilts in the control lines, with four additional gilts used for reserve matings in each line. The plan in all lines was to produce a new generation each year and all gilts were bred to farrow during a single nine-week period starting in August. However, owing to reproductive problems in 1959, 1961 and 1962, some animals (i.e., 17 D–H females, 6 D–L boars, 12 D–L females, 6 Y–H females and 4 Y–L females) were used as parents in two successive years. By mating these animals to young animals belonging to the next higher numbered generation, each line was considered to be represented by only one generation a year. In all lines, matings were made at random with the restriction of no full-sib or half-sib matings. By 1964, when the last pigs included in the study were born, the average inbreeding, calculated by the formula of Wright (1922), had increased from 2% in the Duroc foundation stock to 23, 24 and 15% in the D–H, D–L and D–C lines; and from 1% in the Yorkshire stock to 18, 19 and 16% in the Y–H, Y–L and Y–C lines.

Because of space limitations, 86 litters (i.e., 5 D–H, 7 D–L, 17 D–C, 17 Y–H, 17 Y–L and 23 Y–C), consisting mostly of progeny from reserve matings, were discarded at weaning time. In addition, in each line, all pigs of a particular sex were discarded from a few randomly selected litters. All pigs were self-fed a mixed ration in individual pens with concrete floors from weaning at 56 days of age to the probing weight of about 79.4 kg. The protein and mineral supplement in the ration was fed at the rate of 30, 25 and 17% during the first, second and third 6-week periods, respectively. Beginning with generation one, four to six boars and four to six gilts were randomly designated for slaughter from each line and all slaughter boars were castrated at weaning time or shortly thereafter. The number of pigs, litters, dams, and sires represented in the study are given in table 1. Each breed-line-generation-sex subgroup was represented by approximately 30 to 35 individuals.

The least squares method of fitting constants, as outlined by Harvey (1960), was used to evaluate sex, generation and line, and sex by line interaction effects for each breed. Simultaneously, partial regressions on pig's date of birth and pig's inbreeding were obtained for each line on a within-generation basis. The least squares analyses included all data collected through the first eight generations for the Duroc lines and the first six for the Yorkshire lines. Since the sex by line interaction was not significant in either breed, the data were reanalyzed, deleting this interaction from the original models. The individual observations were then adjusted to a level equivalent to the unweighted mean of boars and gilts, using the sex constants obtained in the second set of analyses. The means with overall standard deviations for the two continuous variables considered in the study are given in table 2.

TABLE 1. TOTAL NUMBER OF SIRES, DAMS, LITTERS AND PIGS BY BREED AND LINE[a]

Group	Duroc			Yorkshire		
	High-fat	Low-fat	Control	High-fat	Low-fat	Control
Sires	54	50	85	45	45	67
Dams	100	94	106	85	81	82
Litters	107	100	106	88	82	82
Pigs probed	652	579	698	560	522	545

[a] Numbers do not include foundation pigs.

TABLE 2. MEANS AND STANDARD DEVIATIONS FOR INDEPENDENT VARIABLES BY BREED AND LINE

Breed	Variable	Line					
		High-fat		Low-fat		Control	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
Duroc	Day of year born (days)	244.4	13.4	253.2	19.3	240.7	14.5
	Pig's inbreeding (%)	10.3	7.8	10.7	7.5	7.0	4.7
Yorkshire	Day of year born (days)	249.1	16.2	243.0	15.6	245.4	15.6
	Pig's inbreeding (%)	10.0	6.0	10.2	6.5	8.6	5.2

Results and Discussion

The Foundation Populations. Backfat probes on the 82 Duroc and 113 Yorkshire foundation pigs averaged 3.8 and 3.2 cm., respectively. The mean difference of 0.6 cm. between the two breeds was highly significant. The standard deviations were 0.56 cm. for the Durocs and 0.31 cm. for the Yorkshires. The positive correlation between means and standard deviations indicated by these data suggests the presence of scale effects. However, after eliminating the influence of differing means, the coefficient of variability was still higher for the Duroc pigs, i.e., 14.8 *vs.* 9.6%, indicating that scale effects alone did not account for the greater phenotypic variability shown by the Durocs.

Least Squares Constants. The estimates of certain of the effects considered in the least squares analyses are presented in table 3. Sex differences were highly significant and of about the same magnitude in the two breeds. Boars averaged about 0.2 cm. less backfat than gilts, and gilts about 0.2 cm. less than barrows. The differences between boars and gilts agree fairly well with the mean difference of 0.3 cm. reported by Hetzer *et al.* (1956) for similar weight pigs from seven inbred lines, but the differences between gilts and barrows found here are considerably greater than that observed in the earlier study.

Although only three of the six individual line regression coefficients on date of birth differed significantly from zero, the mean regression over all lines was highly significant in both breeds. In all Duroc lines pigs born late in the season tended to be leaner than pigs farrowed earlier, whereas in the Yorkshire lines the situation appears to have been reversed. The results thus suggest a breed by environment interaction.

TABLE 3. LEAST SQUARES CONSTANTS FOR SEX, AND PARTIAL LINEAR REGRESSIONS OF BACKFAT THICKNESS (CM.) ON DAY OF YEAR BORN AND PIG'S INBREEDING IN DUROC AND YORKSHIRE LINES[a]

Item	Duroc	Yorkshire
Sex		
Boar	—.231	—.237
Gilt	0.017	—.048
Barrow	0.214	0.285
Sex differences	——**	——**
Regression on—		
Day of year born (days)		
High line	—.001	0.001
Low line	—.002*	0.001
Control line	—.005**	0.003**
Mean	—.003**	0.002**
Line differences	——	——
Pig's inbreeding (%)		
High line	—.045**	0.012
Low line	0.001	—.019*
Control line	—.026**	—.004
Mean	—.023**	—.004
Line differences	——**	——*

[a] Significance of sex differences, individual regressions and differences in regressions among lines are indicated by a dash for lack of significance, by * for P<.05, and by ** for P<.01.

Over all lines, there was a tendency for backfat thickness to decrease with inbreeding in both breeds, although only for the Duroc lines was the mean regression coefficient large enough to be significant. However, in both breeds the regressions on inbreeding differed significantly among lines. In the D–H line backfat thickness was significantly decreased by inbreeding, while in the D–L line there was a small, although nonsignificant, increase with inbreeding. In contrast, backfat thickness in the Y–H line showed a moderate, although nonsignificant, increase with inbreeding, while in the Y–L line there was a significant decrease. Despite the lack of significance of the regressions in the D–L and Y–H lines, the differences in inbreeding effects between both the D–H and Y–H lines, and the D–L and Y–L lines appear to be real and not to be attributed to sampling errors. The reasons for these differences are not clear. However, the results would seem to suggest that there are dominant genes for both high and low fatness and that the frequencies of the two kinds of genes or their dominance levels differed in the two foundation populations. King and Roberts (1959), in a study of inbreeding effects involving 85 inbred Large White lines found that backfat thickness tended to decrease with inbreeding within lines, while on a between-line basis there was a tendency for the more highly inbred lines to be fatter than average.

Responses to Selection. The generation means of backfat thickness for the selected and control lines are shown in figure 1. In view of the 2-year difference between the time the Duroc and Yorkshire lines were established, the means for the two sets of lines were placed so that they would be comparable with respect to environmental fluctuations between years.

Except for a decline in the first generation in the D–C line, there was a gradual increase in both the D–C and Y–C lines during the earlier generations, followed by a fairly consistent decline thereafter. Actually, the linear regression on generation number was positive but nonsignificant, in the D–C line (b=

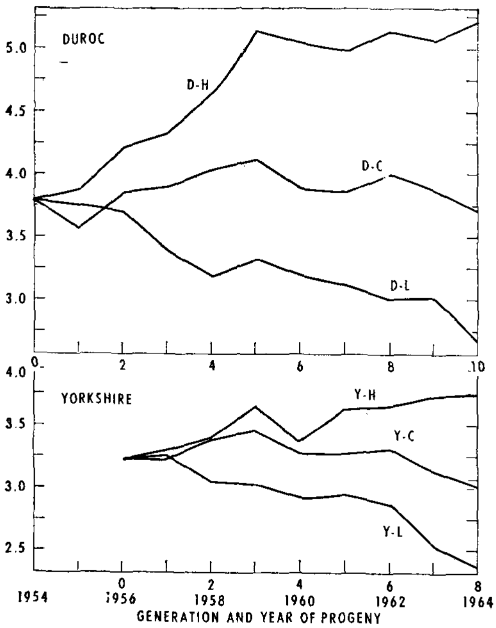

Figure 1. Generation means of selected and control lines.

0.007±0.005), while in the Y–C line it was negative and highly significant (b=—0.018± 0.005). The deviations from linear regression, on the other hand, were highly significant for both lines. Although genetic drift combined with genotype by environment interactions might account for the observed results, the remarkable parallelism in trends shown by the D–C and Y–C lines throughout the experiment suggests that time trends in environmental effects were primarily responsible. The consistency with which year-to-year fluctuations in the selected lines tended to parallel those in the control lines gives added support to this explanation. Expressing each generation mean of the selected lines as a deviation from contemporary controls was thus considered to afford a reliable means for measuring the effectiveness of the selection practiced.

As shown in figure 1, progress in both the D–H and D–L lines appears to have been somewhat greater during the first than during the second half of the experiment. The two lines differed by about 1.8 cm. in generation 5, and by about 2.6 cm. in generation 10. The latter difference is about 4.7 times the phenotypic standard deviation in the foundation population and represents a 38% increase in the D–H line and a 30% decrease in the D–L line. Progress in the Y–H line, on the other hand, appears to have been somewhat slower during the first than during the second half of the experiment while in the Y–L line the situation appears to have been reversed. The two lines actually differed by about 0.5 cm. in generation 4, and by about 1.4 cm. in generation 8. The latter difference is about 4.6 times the phenotypic standard deviation in the Yorkshire foundation population and corresponds to a 17% increase in the Y–H line and a 27% decrease in the Y–L line.

Because of differences in selection intensity both between generations and between lines, a more critical summary of selection responses is provided by plotting the generation means against the cumulative selection differentials. These responses, expressed as deviations from respective controls are shown in figure 2. Selection differentials were calculated as the difference between the mean of animals selected as parents and the mean of the generation to which they belong, weighting the selection differential for each parent according to the number of probed progeny it contributed to the next generation.

Perhaps the most interesting point about figure 2 is that in both breeds selection differentials were generally lower for the low-fat than for the high-fat lines, averaging 0.24 and

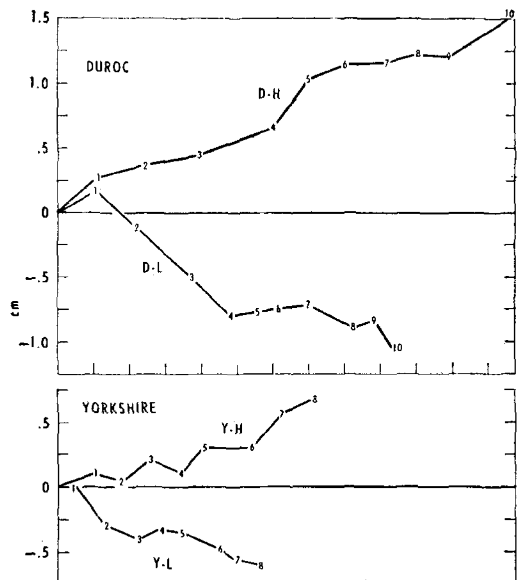

Figure 2. Selection responses relative to contemporary controls plotted against cumulative selection differentials.

0.18 cm. for the D–L and Y–L lines and 0.31 and 0.22 for the D–H and Y–H lines. Apparently, scale effects did not play a major role, for, when measured in standard deviations, the ratios of the differentials obtained for the high and low lines differed only slightly from those based on the original values. If natural selection favored the less extreme phenotypes, the realized differentials would be lower than the expected ones. Actually, the two sets of differentials agreed very closely in all lines, indicating that differential fertility associated with individual intra-generation differences in fatness played no part in either set of lines. However, in both breeds there was a somewhat higher mortality among low-fat pigs. Thus, only about 96.3 and 95.0% of D–L and Y–L pigs completed the test, compared with 99.1 and 97.2% for D–H and Y–H pigs, and 97.0 and 97.2% for D–C and Y–C pigs. Since equal numbers of pigs generally were saved for breeding in each line, the lower differentials obtained for the low-fat lines thus would appear to be partly a consequence of selecting larger proportions of pigs for replacement in these lines and, hence, of using pigs deviating less from the mean of their group than was the case in the high-fat lines.

Table 4 gives the realized heritabilities obtained for the selected lines over both the first and second half of the experiment, as well as for the entire period. Linear regressions were fitted to the points in figure 2, weighting each generation mean by $(n_{Si}\ n_{Ci})/n_{Si}+n_{Ci}$, where n_{Si} and n_{Ci} are, respectively, the number of select and control line pigs in the i-th generation. The slope of the regression line is then the realized heritability, as first suggested by Falconer (1955).

The heritabilities for the D–H and D–L lines were considerably higher for the first than for the second half of the experiment. The regressions underlying the estimates for

TABLE 4. REALIZED HERITABILITY ESTIMATES FROM SELECTION RESPONSES EXPRESSED AS DEVIATIONS FROM CONTROLS

Breed	Generations of selection	Line: High-fat	Line: Low-fat	Line differences[a]
Duroc	0–5	0.48±0.04[b]	0.73±0.06[c]	**
	5–10	0.29±0.06	0.30±0.08	*
	0–10	0.47±0.02[c]	0.48±0.02[c]	*
Yorkshire	0–4	0.13±0.07	0.64±0.08[b]	**
	4–8	0.60±0.07[c]	0.46±0.09	*
	0–8	0.38±0.03[c]	0.43±0.03[c]	*

[a] * P>.05; ** P<.01.
[b, c] Regression of selection response on cumulative selection differential deviates significantly from straight line at 5% and 1% level of probability, respectively.

the entire period showed a highly significant departure from linearity in both lines. The results suggest that in both lines there was a decline in the additive genetic variance, no doubt due partly to a tendency for increasing numbers of genes controlling backfat thickness to be fixed as inbreeding increased. However, neither of the two lines appears to have reached a plateau as yet. During the early generations, the heritability obtained for the D–L line was significantly higher than the one for the D–H line. However, the estimates were almost identical for the later generations, as well as for the entire period.

As in the Duroc lines, the heritability for the Y–L line was somewhat lower for the second than for the first half of the experiment, whereas in the Y–H line the picture was reversed. Also, but apparently for different reasons, the regressions underlying the estimates for the entire period showed a highly significant departure from linearity in both lines. During the early generations, the estimate for the Y–L line significantly exceeded the one for the Y–H line, while both during the later generations and the entire period the estimates did not differ appreciably.

The heritabilities of 0.48 and 0.43 found here for the D–L and Y–L lines over the entire experiment agree rather well with the values of 0.54 and 0.43 which Gray *et al.* (1965) reported from five generations of selection for thinner backfat in two lines of Poland China swine. However, the estimates of these workers are not strictly comparable with the present ones, for they did not maintain a control population. The estimate of 0.29 obtained by Dillard (1963) from comparison of select and control groups is considerably lower than those of the present study.

Other things being equal, the significantly greater selection response of the D–L over and the D–H line and of the Y–L over the Y–H line during the early generations, might be attributed to three causes: (1) a tendency for backfat thickness to be progressively reduced by inbreeding; (2) a lower gene frequency in the base population of genes acting in the downward direction; or (3) directional dominance, in the sense that dominant genes for low fatness were less numerous or had greater effects than dominant genes acting in the other direction. Admittedly, the available evidence does not permit distinguishing between the latter two possible causes of asymmetry. However, the asymmetrical responses shown by both the Duroc and Yorkshire lines are in the direction expected on the basis of the differences in the regressions on inbreeding in table 3. Thus, the results for the Duroc lines indicate that inbreeding reduced progress in the D–H line much more than in the D–L line, hence the apparently greater selection response in the downward direction. In the Yorkshire lines, on the other hand, inbreeding apparently favored selection more in the downward than in the upward direction. Thus, despite the differences in inbreeding effects between the selected Yorkshire and Duroc lines, the signs and relative magnitude of the regressions on inbreeding in the two sets of lines were such that inbreeding might reasonably be held to have contributed to the asymmetry in both sets.

In view of the probably significant differences between some of the lines in date of birth and pig's inbreeding (see table 2), it is of interest to determine how the responses shown by the selected lines would have compared had it been possible to exercise experimental control over these variables. To this end, the observations for each line were adjusted first, to mean date of birth of controls and second, to mean date of birth of controls and zero inbreeding, using the partial within-generation regressions that were obtained for that line (see table 3). Realized heritabilities were then calculated from each of the two sets of adjusted data by the same methods and for the same generation periods as those in table 4. Adjustment of the data for date of birth alone did not materially reduce the asymmetry in selection response between either the D–H and D–L or the Y–H and Y–L lines during the first half of the experiment. However, when the data were also adjusted for inbreeding, the difference in the heritabilities between the D–H and D–L during the first half of the experiment decreased from 0.25 to 0.14, indicating that the differences in inbreeding effects were at least partly responsible for the asymmetry in selection response shown by these lines. In contrast, adjustment for inbreeding effects did little to reduce the asymmetry shown by the selected Yorkshire lines during the first half of the experiment.

Also, for the D–H and D–L lines the realized heritabilities based on data adjusted for date of birth and pig's inbreeding were in each case larger than the corresponding ones in table 4, while the reverse was true of those for the Y–H and Y–L lines. These results agree with those expected on the basis of the observed differences in inbreeding effects. However, for all lines the regressions underlying the realized heritabilities based on adjusted data continued to deviate significantly from a straight line.

Coefficients of Variation. The phenotypic variability of backfat thickness was expressed as the coefficient of variation in order to minimize any effects changing means had on standard deviations. The results, presented in figure 3, show a rather marked decline in

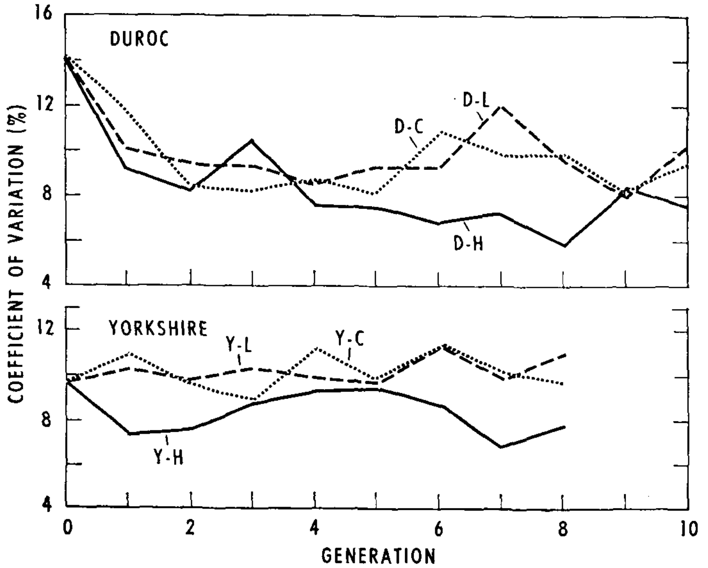

Figure 3. Coefficients of variation in the selected and control lines.

variability in all three Duroc lines during the first two generations. Thereafter there was a tendency for the variability to increase in the D–L and D–C lines, although in both lines the trend was reversed during the last three or four generations. The variability in the D–H line, on the other hand, continued to show a slight downward trend and generally remained below that in the D–L and D–C lines. The variability shown by the Yorkshire lines fluctuated less than in the Duroc lines, but the line differences tended to point in the same direction in the two breeds. The average coefficients of variation obtained by weighting each generation according to the number of pigs probed were, respectively, 7.9, 9.5 and 9.2% for the D–H, D–L and D–C lines; and 8.1, 10.2 and 10.1% for the Y–H, Y–L and Y–C lines. Thus, only in the case of the high-fat lines do the results suggest a decline in phenotypic variability. Further experimentation would seem necessary to determine the nature of these differences.

Heritabilities from offspring—midparent regressions. In addition to the realized heritabilities, estimates of the heritability of backfat thickness were obtained from the regression of offspring on midparent means, using the data that provided the estimates in table 4. All regressions were calculated on a within-generation basis, repeating the record on a midparent for each of their offspring. The heritabilities obtained are presented in table 5.

The estimates varied considerably between both lines and generation periods. In both breeds the estimate for the low-fat line significantly exceeded the one for the respective high-fat line during the early generations. The line differences were reversed during the second generation period, but for neither this period nor the entire period did the estimates differ significantly among lines. The estimates for the control lines were intermediate except for the second generation period and the entire period in the Durocs in which they slightly exceeded those for the selected lines. Also, only in the D–L and the Y–H lines did the heritabilities differ significantly between the two generation periods.

Comparison of the heritabilities for the selected lines in table 5 with those based on selection responses in table 4 shows that only in the case of the Y–L line over the entire period did the estimates differ significantly between methods. Heritability estimates based on regression of offspring on midparent could include variance due to epistatic gene effects and maternal effects in addition to additive genetic variance. Realized heritabilities, on the other hand, reflect almost exclusively the fraction of variance attributable to strictly additive gene effects. Thus, even though the heritabilities from offspring-midparent regressions generally exceeded those based on selection responses, epistatic and/or maternal effects do not appear to have contributed materially to the variation in backfat thickness in these lines. As in the case of the realized heritabilities, it also appears that most of the corresponding offspring-midparent estimates for both selected and control lines did not differ appreciably between breeds. Thus, backfat thickness would seem to be about equally heritable in the breeds studied here.

Summary

Selection for both high and low backfat thickness was carried through 10 generations in two Duroc lines and through eight generations in two Yorkshire lines. An unselected control line derived from the same sources as the selected lines was maintained in each breed.

After 10 generations of selection, the high-

TABLE 5. HERITABILITY ESTIMATES FROM WITHIN-GENERATION REGRESSIONS OF OFFSPRING ON MIDPARENT MEANS

Breed	Generations of selection	Line: High-fat	Low-fat	Control	Line differences[a]
Duroc	0–5	0.40±0.10	0.79±0.11	0.70±0.07	*
	5–10	0.45±0.10	0.34±0.13	0.48±0.11	**
	0–10	0.43±0.07	0.60±0.08	0.62±0.06	**
Yorkshire	0–4	0.24±0.13	0.78±0.09	0.58±0.11	*
	4–8	0.76±0.14	0.51±0.14	0.59±0.09	**
	0–8	0.49±0.10	0.70±0.08	0.58±0.07	**

[a] ** P>.05; * P<.05.

and low-fat Duroc lines differed by 2.6 cm. or 68% of the initial mean. The corresponding difference between the two selected Yorkshire lines after eight generations was 1.4 cm. or 44%.

Least squares analyses revealed significant line differences in inbreeding effects in both breeds. In the high-fat Duroc and low-fat Yorkshire lines backfat thickness was significantly decreased by inbreeding, while in the low-fat Duroc and high-fat Yorkshire lines there was a small, although nonsignificant, increase with inbreeding.

Realized heritabilities calculated from regressions of generation means on cumulative selection differentials were 0.47 and 0.48 for the high- and low-fat Duroc lines and 0.38 and 0.43 for the high- and low-fat Yorkshire lines. Selection response in the high- and low-fat Duroc lines and the low-fat Yorkshire line declined significantly as the experiment progressed, whereas the reverse was true for the high-fat Yorkshire line.

Phenotypic variability, as measured by the coefficient of variation, decreased slightly in the high-fat lines, but showed no material change in the low-fat lines or the control lines.

Adjustment of the data for differences in date of birth and pig's inbreeding reduced somewhat the asymmetry in selection response shown by the high- and low-fat Duroc lines during the first half of the experiment but failed to do so in the case of the selected Yorkshire lines.

Estimates of heritability from regressions of offspring on mid-parent means were generally in good agreement with those based on selection responses. Thus, epistatic and/or maternal effects probably contributed little if anything to the variation of backfat thickness. It is concluded that the selection practiced was rather highly effective in both the upward and downward direction and that the heritability of backfat thickness is of about the same magnitude in Duroc and Yorkshire swine.

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