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Evaluation of Selection in Developing Inbred Lines of Swine

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in collaboration with
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Agricultural Experiment Stations of Illinois, Indiana, Iowa, Minnesota, Missouri, Nebraska, Oklahoma and Wisconsin and U. S. Department of Agriculture cooperating.

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THE PROBLEM

Selection is the process of discrimination by which individuals of divergent phenotypes are made to differ in rate of reproduction. By this means nature has improved the adaptability of wild populations and man has improved the performance of his domesticated animals and plants. The effectiveness of selection between (if not always within) species during the long periods of time available for evolutionary change is unquestioned. Of course, it is obvious that selection can be effective only in the presence of genetic variability between individuals or populations, and that this variability springs from segregation and recombination within heterozygous populations, augmented by such forces as mutation, chromosomal rearrangement, hybridization, inbreeding, and random drift in gene frequencies. By definition, however, selection tends to be the non-random and hence the guiding element that produces genetic changes in large populations.

Evidence has been presented that several important economic characters of livestock have been improved steadily (Lush, 1951). Presumably this was accomplished mainly by selection. This evidence indicates that unimproved foundation stock can be improved rapidly for a time by consistently selecting the superior individuals from each generation as the parents of the next generation. There is more uncertainty concerning the rate of improvement to be expected from continued selection within stocks that have already reached a high level of performance through previous generations of similar selection. It has been suggested (Wright, 1930; Lush, 1937; Hull, 1945; Wright and Dobzhansky, 1945; Dickerson, 1951) that the effectiveness of continued selection for net or total performance may decline steadily, finally reaching a state of near-equilibrium, even though total genetic variability remains high.

The genetic improvement obtained each generation from selection is equal to the superiority in the average effects of the genes carried by the parents selected to produce the next generation, compared with unselected members of the generation from which they were chosen. In the simplest case of selection for a single character, directly, the genetic gain is the product of the parental superiority in phenotype (i.e., of the individual, its family or progeny) and the effective heritability of variation in the phenotypic measure of performance. The phenotypic superiority of selected parents (the selection differential) is limited by the natural rate of reproduction or proportion of off-spring which must be selected as parents. The selection differential for any one character also is limited by the attention given, consciously or unconsciously, to other traits in selecting the parents and is affected by the degree of phenotypic correlation with such other traits. The effective heritability of differences in phenotype is limited both by the uncontrolled environmental variation and by any genetic variation that is uncorrelated with the average effects of genes (e.g. dominance and epistatic deviations from average gene effects). Even small negative genetic correlations between factors considered in making selections could reduce effective heritability of net merit sharply, even though heritability of individual factors remained high. The relative magnitude and signs of genetic, as compared to enviromental, correlations between traits also influences effective heritability, as will be shown later.

Selection within mildly inbred lines has received major emphasis in the cooperative research of the Regional Swine Breeding Laboratory, which began in 1937. In numerous earlier attempts to develop inbred lines by intensive inbreeding (McPhee, *et al.,* 1931; Hughes, 1933; Godbey and Starkey, 1932; Hodgson, 1935; Willham and Craft, 1939; Lush, *et al.,* 1948), selection usually had been unable to prevent a serious decline in fertility, prolificacy, viability and growth rate. Only a few of these highly inbred lines survived for as many as 8 or 10 generations (Hughes, 1933; Hodgson, 1935). The only one still in existence has been maintained since the 8th generation by mild inbreeding after crossing of two sublines (Winters, *et al.,* 1943). The ineffectiveness of selection within selfed lines of corn had been shown previously (Richey, 1925).

Under the assumption that inbreeding reduced performance primarily because of the increase in proportion of homozygous recessive individuals, it seemed reasonable that careful selection might prevent much of the inbreeding depression if the rate of inbreeding were slow (Lush, *et al.,* 1948). Wright's (1922b, 1949) analyses and interpretation of results from inbreeding in guinea pigs encouraged this approach. During the decade from 1937 to 1947 more than 40 inbred lines were developed within five breeds and three crossbred foundation stocks. Although the intensity of inbreeding varied, inbreeding was relatively slow in all cases, usually 2 to 4 percent per generation.

The present cooperative study was undertaken in 1947 to determine the amount and kind of selection actually applied and compare actual with expected rates of improvement during the development of these inbred lines of swine through mild inbreeding. Portions of the results from some of the stations have been reported in abstract form (Laben and Whatley, 1947; Kottman, *et al.,* 1948; Dickerson, 1951). Parallel studies of the Minnesota data also have been made (Fine and Winters, 1952, 1953; Rempel and Winters, 1952).

SOURCE OF DATA

The amount and kind of selection actually applied was calculated for 38 lines developed at seven of the state experiment stations cooperating in the Regional Swine Breeding Laboratory. In all of the lines except those at Illinois, it was intended that each of the economically important characters should receive attention in selection. In the two Illinois Hampshire lines, selection was intended solely for rapid growth in one line and for slow growth in the other (Krider, *et al.,* 1946). The Illinois data are for eight years, 1940 through 1947. At Indiana, the data include a Chester White and a Duroc-Landrace line, covering 1941 through 1948. The Iowa data are for Poland Chinas in eight 1-sire lines and three 2-sire lines from 1938 through 1947 and in one 4-sire line from 1932 through 1947. The Missouri data included three Poland China lines starting in 1938, but in 1943 two were discontinued and one new line of Poland and one of Hampshire were started. Data through 1949 were used. Nebraska included data on 12 lines of Durocs. Six of these were begun in 1938 or 1939 and were discarded or incorporated into new lines between 1942 and 1945. The remaining six were started between 1944 and 1946, and data through 1946 were used. Data from the four Oklahoma Duroc lines were used during the years 1939 through 1947; one of these lines was discontinued and another founded in 1943. The Wisconsin line of Chester Whites was founded in 1942. It was divided into two sublines in 1944 and into three sublines in 1946; the data included records from 1942 through 1948.

The effectiveness of selection was studied in data from the Iowa, Minnesota, Missouri, Nebraska, and Oklahoma projects, using time trends in performance within lines. Comparisons of linecrosses with the parental inbred lines at four stations (excluding Missouri) were used to obtain estimates of decline in performance due to the inbreeding rise. The Minnesota data included 14 lines of Poland China and two lines developed from crossbred foundations for the period 1938 through 1948.

CHARACTERS STUDIED

The superiority of individuals used as breeding animals and the time trends in performance were calculated for a number of the economically important traits of swine. The productivity of sows was measured by size of litters farrowed and weaned and by the average weaning weight per pig in the litter; the growth rate of pigs was measured by their weights at 56 and at 154 days of age. Scores ranging from 1 to 9 for each of six aspects of live animal conformation at market weight were summed to obtain a "total" score for desirability of conformation (Stonaker and Lush, 1942). In addition, nine other descriptive scores proposed by Phillips et al.[1] were recorded and included in the data studied by some of the stations. Wright's (1922a) coefficient of inbreeding was calculated for both the dams and their litters and was used to learn whether selection favored or discriminated against heterozygosity. Data concerning efficiency in use of feed and composition of carcasses were not included, because they were available only for some samples of the population and in some of the years.

ADJUSTMENT OF DATA

Since computation of the mean superiority of selected parents involved comparing litters from sows of different ages, the size and weight of litters from older sows were adjusted to a gilt (1.0 year of age) farrowing basis, as shown in Table 1. These corrections were based on results reported by Lush and Molln (1942) for herds of swine maintained at a number of state and federal experiment stations. Data from Indiana were an exception. There, the factors used were based on analysis of age of

TABLE 1 -- PROCEDURE USED TO ADJUST SIZE AND WEIGHT OF LITTERS FROM OLDER SOWS TO THEIR EQUIVALENT FROM GILTS AT ONE YEAR OF AGE[1/]

Actual age of sows in years	Adjustment of Actual Record			
	Litter Size (pigs)		Litter Weight Weaned (lbs.)	
	Born N_b	Weaned N_w	Total T_w	Per Pig $\overline{W}$
1.5	-0.5	-0.5	$-(20 + \frac{T_w}{10})$	$\frac{\text{Adj. } T_w}{\text{Adj. } N_w}$
2.0	-1.5	-1.0	$-(20 + \frac{T_w}{10})$	$\frac{\text{Adj. } T_w}{\text{Adj. } N_w}$
2.5	-1.5	-0.5	$-(20 + \frac{T_w}{10})$	$\frac{\text{Adj. } T_w}{\text{Adj. } N_w}$

[1/] Except that Indiana records of sows 1.5 years or older were multiplied by 0.7 for N_b, N_w and T_w in the W.K. Chester White line, and by .7 for N_b but by .6 for N_w and T_w in the Landroc line.

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[1] Phillips, R. E., H. O. Hetzer and R. L. Hiner. 1940. Relation of scores of swine to carcass yields and certain carcass measurements. Res. Item 15, Regional Swine Breeding Lab., USDA. (Not available)

dam effects within each of the two lines separately. Since only gilt litters were produced in the Illinois data used, no age adjustment was needed in figures from that State. Age of dam has some influence on individual pig weights at 56 days but less at 154 days; the increased weight of litters from older sows was due both to the increase in number of pigs weaned and to heavier weights per pig weaned. No adjustment was made for the influence of the dam's age on individual pig weights, except in the Iowa data where 56-day weights of pigs from sows 1½ years of age or older were multiplied by a factor of 0.877. No correction was made for variation in age of gilts when their first litters were farrowed, although Stewart (1945a) has shown that such variation has an important influence on the litters produced. Hence, variation in litter performance arising from differences among gilts in age at farrowing remained in the data as uncontrolled non-genetic variability.

MEANS AND STANDARD DEVIATIONS

The means given in Table 2 indicate the levels of inbreeding and of performance for the lines within which selection was studied.

Inbreeding generally ranged from nearly zero in the first generations to between 30 and 60 percent during the last years included in this study. At some stations, such as Iowa, inbreeding was initially higher because part of the lines were started by subdividing strains that were already moderately inbred. The rate of inbreeding in a line varied with the number of sires and the number of females used each year to produce replacements. Inbreeding was most rapid in the one-sire lines at the Iowa station. It was least rapid in the Illinois lines, where five sires, each from a different litter, were mated to the least related females of the same generation.

The effects of inbreeding are responsible, at least in part, for the generally unimpressive levels of performance, as will be shown later. However, it should be remembered that the means in Table 2 represent gilt litters or their equivalent, and that all litters farrowed were included even though no pigs survived in some. Size of litters farrowed averaged 7.5 pigs, but 40 percent of the pigs died before weaning, leaving an average of only 4.5 pigs per litter at 56 days of age. The average weanling pig weight, giving equal weighting to each litter, was 27 pounds after correction to the gilt litter basis. The actual average weight, giving equal attention to each pig weaned, was higher, 29 pounds, since about 40 percent of all litters were produced by older sows. Although not high, the mean 154-day weight of 132 pounds showed somewhat less effect of inbreeding than did size and weight of litters weaned. The extent to which inbreeding depressed performance will be considered in a later section.

TABLE 2 -- MEANS AND STANDARD DEVIATIONS[1] BY STATIONS

A. Inbreeding and Litter Performance

Station	Lines	No. line-seasons	No. of litters	Inbreeding Percentage Dams Mean	Dams S.D.	Litters Mean	Litters S.D.
Illinois	2 Hamp.	14[2]	178	4	--	4	--
Indiana	1 C.W. 1 D-L	17	363	20	8	28	3
Iowa	12 Poland	202	2063	24	6	28	6
Missouri	2 Poland 1 Hamp.	26	453	14	6	20	7
Nebraska	12 Duroc	95	858	20	11	23	10
Oklahoma	4 Duroc	53	407	--	--	16	--
Wisconsin	3 C.W.	14	199	6	7	14	8
Total or Wt'd. Mean[3]	38	421	4521	21	7	24	7

Station	Litter Size-Pigs[4] Born (N_b) Mean	Born S.D.	Weaned (N_w) Mean	Weaned S.D.	Litter Weight Weaned - lbs.[4] Total (T_w) Mean	Total S.D.	Per pig (W) Mean	Per pig S.D.
Illinois	7.15	2.38	4.63	2.51	109.0	59.3	(23.7)	(4.16)
Indiana	8.33	2.37	4.72	2.45	149.4	83.8	(31.8)	(6.20)
Iowa	6.78	2.30	3.96	2.21	113.1	65.5		
	(6.95)	(2.18)	(4.42)	(1.95)	(126.2)	(58.9)	(28.0)	(7.14)
Missouri	7.82	2.39	5.38	2.35	147.2	64.1	(28.0)	(6.63)
Nebraska	8.05	3.01	4.61	2.72	132.3	80.9	(29.0)	(7.54)
Oklahoma	8.45	2.96	5.50	2.58	136.6	67.1	(24.8)	
Wisconsin	9.00	2.70	4.90	2.90	121.4	73.6	(24.8)	
Total or Wt'd Mean[3]	7.50	2.57 (2.44)	4.48	2.42 (2.14)	124.2	69.9 (62.8)	(27.3)	(7.05)

B. Individual Pig Weights, in Pounds, and Index

Station	At 56 days (W56) No. of pigs	Mean	S.D.	At 154 days (W_{154}) No. of pigs	Mean	S.D.	Index[5] Mean	S.D.
Illinois	824	23.9	6.2	722	101.9	28.0		
Indiana	2012	31.9	8.8	1817	153.8	31.6		
Iowa	8684	29.0	7.2	7142	133.9	26.7	(190)	(31.8)
Missouri	2466	28.7	6.8	2022	135.2	22.4		
Nebraska	4176	30.6	7.5	3545	135.2	35.9		
Oklahoma	2441	27.1	7.4	1272	119.8	31.7		
Wisconsin	1027	25.9	9.8	847	118.3	26.7		
Total or Wt'd. Mean[3]	21,650	29.0	7.4	17,377	131.7	29.3		(34.9)[6]

[1] Among all litters farrowed (A) or all pigs measured (B and C) within a line and season. Figures in parentheses (A) include only litters in which one or more pigs were weaned.

[2] Eight seasons for the "Rapid" and 6 seasons for the "Slow" growing line.

[3] Each station mean weighted by the number of line-seasons.

[4] All records for sows farrowing at one year of age, or the equivalent. See Table 1.

[5] Index = $2 \left(N_b + 2\,N_w + \frac{2\,T_w}{30}\right) + W_{154}$

[6] Estimated roughly from the actual standard deviation of 31.8 among pigs with 154-day weights at the Iowa station, substituting the larger standard deviations typical of all stations.

TABLE 2 -- (CONTINUED)
C. Scores for Conformation of Live Animals at Market Weight[7]

Station	Illinois		Iowa		Missouri[8]		Oklahoma		Total or Wt'd. Mean	
No. Line-Seasons	14		89				44			
No. Pigs	728		3550		5		1549		138[7]	
Score	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
General:										
Vigor	6.84	1.67	6.64	1.00	7.58	1.04	7.14	1.22	6.83	1.07
Quality	6.58	1.25	6.65	0.62	7.23	1.24	6.28	1.00	6.55	0.76
Body length	6.50	1.24	6.47	0.66	5.87	1.12	5.87	0.85	6.26	0.74
Details	6.00	1.27	6.00	1.00	6.43	1.16	5.81	0.99	5.96	1.00
As whole	5.97	1.37	6.11	1.00	5.57	1.89	6.24	1.21	6.13	1.10
Market grade	5.96	1.46	6.56	1.03	7.70	0.88	7.43	1.36	6.88	1.13
Total	37.83	7.62	38.41	4.36	40.38	5.91	38.76	5.79	38.59	4.87
Descriptive:										
Head	6.79	1.21			3.34	0.48				
Shoulders	6.61	1.22			5.67	1.98				
Arch back	6.06	1.11			5.23	0.86				
Slope rump	5.85	1.10			6.04	1.58				
Leg length	6.51	1.22			5.33	1.15				
Body depth	6.18	1.27			7.24	1.03				
Ham plumpness	4.88	1.41			5.81	1.48				
Shape back	5.90	1.25			6.63	1.19				
Body width	5.62	1.33			6.04	1.32				

[7] At a live weight of 200 to 240 pounds, except at Illinois, where scores were given at either 180 or 154 days of age. Illinois data were omitted from the weighted mean for all stations.

[8] Individual scores for 79 Poland China Line II pigs in 1940, but total scores for 305 Line II pigs in 5 seasons 1939-1942.

The standard deviations given in Table 2 indicate the amount of variation among individuals within the same line and in the same season. They show roughly the opportunity for selection. They also provide a basis for expressing the mean superiority of the breeding animals selected in terms of standard deviation units, to permit comparisons of selection intensities among different characters and with expected maxima.

The degree of inbreeding varied rather widely between litters within the same line and season. The range, computed as four times the standard deviation, varied from 24 to 40 percent among the five stations where the calculations were made (i.e. ± 12 to 20 percent from the mean). This variation provided ample opportunity for selection against the more highly inbred litters if inbreeding really depressed performance in the characters which were the primary objects of selection.

Variability relative to the mean was much greater for size and weight of litters than for weights or scores of individual pigs. The coefficient of variation averaged 34 percent for number farrowed, 54 for number weaned, 56 for total weight of litters, but only 26 percent for litter average weaning weight per pig[2], 26 percent for individual weaning weights, 22 percent for pig weight at 154 days, and 13 percent for total scores of conformation for individual pigs. With few exceptions, the coefficient of variability for a given trait was very similar at different stations.

OPPORTUNITY FOR SELECTION

The proportion of the progeny which is required for replacement of breeding animals directly limits the mean superiority of those selected. (See Table 3.) This fraction, in turn, is governed by the rate of reproduction characteristic of a population. Breeders may modify the replacement rate within limits. They may deliberately increase or reduce the proportions of older animals used for breeding. They also may seek to reduce the proportion of progeny needed for replacements by attempting to increase the rate of reproduction itself (i.e. fertility, prolificacy, and viability). Deliberate use of more boars than necessary in order to minimize inbreeding would reduce opportunity for selection among the boars. However, allowing greater use of the better young boars among those saved could increase average superiority of parents somewhat, compared with equal use of each boar.

The number of boar pigs weaned per season within a single inbred line constitutes the maximum population from which replacement boars can be selected. These mean numbers varied from 24 to 59 among the stations. Except for Illinois, where five young boars from five different litters were saved each year to minimize inbreeding, the proportion of weanling boars used ranged from 5 to 9 percent. The mean proportion of 8.3 percent is several times larger than would have been required by the reproductive capacities of the boars, if no attempt had been made to keep the rate of inbreeding mild or if unrelated boars could have been used so that reducing the number of boars would not have increased the rate of inbreeding. It is evident that some sacrifice in the intensity of selection among boars was made in developing these inbred lines of swine, in order to minimize the rate of inbreeding and thus maintain greater genetic variability within the lines each generation.

The much smaller proportion of boar than of gilt pigs retained for use as parents would be expected to provide much greater opportunity for selection among the boars. The average number of gilt pigs weaned per line in years when any were retained as breeders was 27, of which 33 percent were kept to farrow litters. The effect of reproductive

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[2] The coefficient of variation was as large among litter means for 56-day pig weights as among individual pigs, presumably because (1) correction of litter means for age of dam (Table 1) reduced the mean more than the variance, and (2) giving equal weight to each litter mean, disregarding number of pigs in the litter, greatly increased the contribution of intra-litter variation to the variance between litters compared to what it would have been if each litter were weighted according to its number of observations, and also may have reduced the mean.

TABLE 3 -- MEAN NUMBERS AVAILABLE AND PROPORTIONS USED AS BREEDERS PER LINE-SEASON GROUP, FOR EACH SEX AND AGE[1]

	Boar Pigs			Gilt Pigs			Older Boars			Older Sows		
Station	No. Gps.	No. Wn'd	% Used	No. Gps.	No. Wn'd	% Used	No. Gps.	No. Avail.	% Kept	No. Gps.	No. Avail.	% Kept
Illinois	14	30.0	17.1	14	28.8	45.7						
Indiana	14	58.7	5.1	17	59.9	29.4	11	4.45	55.7	11	21.9	39.5
Iowa	143	27.8	8.8	176	23.8	38.2	127	1.70	65.1	170	11.6	47.1
Missouri	20	51.4	5.7	22	45.3	33.6	9	2.78	56.8	18	16.1	59.9
Nebraska	73	24.0	6.5	93	23.0	27.2	32	1.91	75.2	81	8.2	37.5
Oklahoma	46	25.8	9.2	48	24.2	22.0	38	3.53	57.8	50	8.1	61.7
Wisconsin	12	38.7	7.0	14	33.6	36.0	14	3.29	48.0	14	14.2	51.0
Mean[2]	322	30.0	8.3	384	27.0	33.0	231	2.30	63.5	344	11.0	47.6

[1] Only for line-seasons from which some breeders were selected. The proportions of gilt pigs and of sows selected from each line-season were weighted by the numbers of each retained [e.g. for gilts selected:

$$\frac{8\ (31.1) + 10\ (33.5) + \ldots \text{ etc.}}{(\text{Total number of gilts selected in all line-seasons at one station})}\Bigg]$$

The proportions of boar pigs and of older boars chosen from a line-season were weighted by the number of weaned progeny sired by those boars in the following season.

[2] Within each age-sex classification, the mean for each station was weighted by the number of line-season groups from which any breeders were chosen, $\frac{(\text{e. g. } 14\ (17.1) + 14\ (5.1) + \text{etc.})}{322}$

rate, and of the age-composition of the sows used, on the intensity of selection is illustrated by contrasting the 22 percent retained at Oklahoma, where 5.50 pigs were weaned per litter (Table 2) but only 40 percent of the sows used were gilts (Table 4A), with the 46 percent of gilts retained at Illinois, where litter size was 4.63 at weaning and only gilts were used as breeders.

In seasons when some of the sires were retained for use again the following season, the average proportion kept was rather large, 64 percent of the mean of 2.3 sires used. Usually boar replacements were obtained from the spring litters and one or more of those used to sire spring litters were retained to sire the fall litters. Sometimes sows were kept for further use when none of their gilt pigs were retained. In seasons when some tried sows were retained, nearly one-half of the sows (48 percent) were kept. Although less culling was practiced among sows than among gilt pigs, sows could be culled on the basis of their own productivity, whereas only the dam's productivity was available when gilts were chosen. To the extent that the older sows farrowing in a given season tended to be discarded because of age rather than on the basis of performance, the proportion saved among the younger sows would be larger than the 48 percent shown in the table.

SUPERIORITY OF SELECTED PARENTS

The basic measure of selection applied is the selection differential or the mean superiority in performance of the selected individuals compared with the whole unselected population from which they were chosen. It is computed separately for sires ($\triangle$ S) and for dams ($\triangle$ D), because each sex of parents contributes equally to the genetic composition of the progeny although the selection differential may differ radically between sexes. The net selection differential for parents is the unweighted mean of that for the sires and dams, separately (i.e. $\frac{\triangle S + \triangle D}{2} = \triangle P$). This measures only the apparent superiority of the individuals selected as parents of the next generation—their real superiority is determined by the average effects of the genes transmitted by these parents, and that is only a fraction of the selection differential for most characters (i.e. effective heritability, g^2, multiplied by $\triangle$ P).

Annual Selection Differentials

Methods

The effectiveness of selection is measured in terms of improvement per unit of time. Actual selection for a given trait such as litter size in swine is practiced at several ages. The first culling among boar and gilt pigs is based in part on the size of the dam's litter and any genetic improvement resulting from this selection is transmitted to progeny born when the parents are one year of age. If a portion of these same selected sires or dams are retained to produce litters when 1½ or 2 years of age, the improvement per year from the time the parents are born until their average age when their progeny are born is given by (Dickerson and Hazel, 1944b):

$$\triangle G = \frac{N^s{}_1 g^2 S_1 + N^s{}_2\ (g^2S_1 + g^2S_2) + N^d{}_1 g^2 D_1 + N^d{}_2\ (g^2D_1 + g^2D_2)}{N^s{}_1 A^s{}_1 + N^s{}_2 A^s{}_2 + N^d{}_1 A^d{}_1 + N^d{}_2 A^d{}_2} \qquad (1)$$

Where: $N^s{}_1$, $N^s{}_2$, $N^d{}_1$, and $N^d{}_2$ are the proportions of all weaned progeny from each age-sex group of parents; S_1, S_2, D_1 and D_2 are selection differential increments from the first and from the second cullings among boars, and among sows; $A^s{}_1$, $A^s{}_2$, $A^d{}_1$ and $A^d{}_2$ are ages in years for each group of parents, and g^2 is the appropriate degree of heritability in each case.

If the selection differential at each culling is expressed in units having the same degree of heritability, the selection differential applied per year may be computed as follows:

$$\triangle P = \frac{N^s{}_1 S_1 + N^s{}_2\ (S_1 + S_2) + N^d{}_1 D_1 + N^d{}_2\ (D_1 + D_2)}{N^s{}_1 A^s{}_1 + N^s{}_2 A^s{}_2 + N^d{}_1 A^d{}_1 + N^d{}_2 A^d{}_2} \qquad (2)$$

In practice, individual parents may be retained at more than two successive cullings, requiring that the formula for $\triangle P$ be extended to S_n, D_n, $A^s{}_n$, $A^d{}_n$, $N^s{}_n$ and $N^d{}_n$. Ideally, $\triangle P$ should be computed separately by season within a line, and then averaged over all seasons. However, for the purpose of comparing the amount of selection applied at different ages between different lines, sexes, or stations, it is convenient to express selection for each age and sex of parents in terms of "annual selection differentials" obtained by dividing the actual selection differential by the interval of time represented (e.g. $s_2 = \frac{S_2}{A^s{}_2 - A^s{}_1}$, where S_2 is superiority of sires used at ages $A^s{}_2$ over those used at age $A^s{}_1$). Young boars and gilts produce their first progeny at one year of age, so that $S_1 = s_1$. Occasionally, however, some of the boars or gilts will produce their first litters at 1.5 or even at 2 years of age. In such cases, any transmitted effect of the superiority of the selected sires or dams is delayed and the *annual* selection differential is $s_1 = \frac{S_1}{A^s{}_1}$ or $d_1 = \frac{D_1}{A^d{}_1}$.

To obtain mean annual selection differentials for a line, the value for each sex and age-group (e.g. s_2) in a given season was weighted by the number of progeny weaned from those parents in that season. $(\overline{A^s_2})$, the weighted mean age of these selected older sires when their progeny were born was computed similarly, as were the means for s_1, d_1, d_2, A^s_1, A^d_1, A^d_2. The approximate mean annual selection differential for parents of a given line then was calculated as:

$$\triangle P = \frac{\overline{A^s_1}\,\overline{s_1} + N^s_2\,(\overline{A^s_2} - \overline{A^s_1})\,\overline{s_2} + \overline{A^d_1}\,\overline{d_1} + N^d_2\,(\overline{A^d_2} - \overline{A^d_1})\,\overline{d_2}}{2T = \overline{A^s_1} + N^s_2\,(\overline{A^s_2} - \overline{A^s_1}) + \overline{A^d_1} + N^d_2\,(\overline{A^d_2} - \overline{A^d_1})} \qquad (3)$$

This approximation will be quite accurate, unless the mean age of parents (T) changes materially from year to year.

Since $\triangle P = \frac{\triangle S + \triangle D}{2}$, the effective *annual* selection differential for sires is $\triangle S = \frac{\overline{A^s_1}\,\overline{s_1} + N^s_2\,(\overline{A^s_2} - \overline{A^s_1})\,\overline{s_2}}{T}$, and the corresponding one for dams is $\triangle D = \frac{\overline{A^d_1}\,\overline{d_1} + N^d_2\,(\overline{A^d_2} - \overline{A^d_1})\,\overline{d_2}}{T}$.

Results (Table 4)

Age composition of parents: Young boars sired 74 percent of the pigs weaned and gilts produced 60 percent of the litters. These proportions varied between stations from 48 to 84 percent for boars and from 40 to 73 for gilts, except in the Illinois project where only young boars and gilts were used. The rest of the breeders were boars and sows that were at least 1.5 years of age and that had been used as breeders previously. The mean age was 1.81 years for the older sires and 2.02 for the older dams, making the mean age 1.22 years for all sires and 1.44 for all dams and 1.33 years for all parents. The generation interval ranged from 1.21 to 1.46 years between stations. The Minnesota station has reported even longer intervals (Fine and Winters, 1952). In general, using a larger proportion of older boars and sows increases the opportunity for selection in choosing young boar and gilt replacements (i.e. increases S_1 and D_1) but reduces culling among the older boars and sows (i.e. reduces S_2 and D_2). The optimum age composition would be the one at which selection per unit of time for all traits considered is approximately equal for each age among sires (i.e. $s_1 \cong s_2$) and among dams (i.e. $d_1 \cong d_2$).

The present results show that there was little additional culling of boars in choosing those to be used for a second or later breeding season ($s_2 < s_1$) in terms of their dam's productivity, their own growth rate (Table 4A) or conformation at market weight (Table 5A). Attention paid to adult conformation, to progeny performance and to added information on the dam's productivity in selecting the older boars used was not measured. It might justify some use of older sires, even though

TABLE 4A -- ANNUAL SELECTION DIFFERENTIALS FOR YOUNG AND OLDER SIRES (s_1, s_2) AND DAMS (d_1, d_2), WITH PROPORTIONS OF PROGENY WEANED (N) FROM EACH AND MEAN AGE OF PARENTS ($\overline{A}$)

Station No. Line Seasons	Group	N	$\overline{A}$ (yrs.)	Annual Selection Differentials								
				Litters Size[1]		Litter Wt. (lbs.)[1]		Pig Wt. (lbs.)			Inbreeding %	
				N_b	N_w	T_w	$\overline{W}$	W_{56}	W_{154}	Index[1]	Dam	Litters
Illinois	s_1	1.00	1.00	.32	.45	14.6	.48	4.97	24.0	32.6	.32	-.20
"Rapid" 8	d_1	1.00	1.00	.40	.75	21.2	.29	2.88	10.3	23.5	-.03	-.04
"Slow"6	s_1	1.00	1.22	.33	.86	18.4	-.88	-2.81	-28.6	-14.7	-.10	-.40
	d_1	1.00	1.27	.15	.40	5.8	-.69	.38	-9.9	-4.5	.04	-.05
Indiana	s_1	.72	1.08	.48	.74	33.6	1.87	6.28	26.6	42.4	-1.65	-3.51
13	s_2	.28	2.59	-.11	.21	6.1	-.12	-.63	-.9	4.5	.92	-1.70
	d_1	.73	1.05	.30	.69	27.0	1.14	2.66	13.9	22.2	-1.08	-2.40
	d_2	.27	2.28	.49	.84	28.9	-.23	1.23	3.1	6.1	.59	.99
Iowa	s_1	.77	1.03	.38	.81	29.1	1.50	5.92	22.9	38.7	-2.05	-2.17
202	s_2	.23	1.91	.14	.06	7.1	.90	1.15	4.1	7.0	.37	-.61
	d_1	.61	1.05	.25	.55	18.8	.83	2.46	13.2	23.6	-.98	-.85
	d_2	.39	2.13	.35	.64	19.5	1.47	.81	5.1	16.8	-.20	-1.12
Missouri [2]	s_1	.84	1.03	.26	.44	17.4	.92	5.75	23.2	32.4	-.35	-1.40
36 (26)	s_2	.16	1.76	.25	.62	12.5	-.96	-1.06	11.3	20.6	-1.00	-8.73
	d_1	.71	1.01	.16	.42	15.1	.54	2.70	11.1	19.1	-.11	-2.27
	d_2	.29	1.90	.74	.67	22.6	1.26	1.59	6.1	20.4	-.08	-1.74
Nebraska	s_1	.78	1.04	.19	.55	23.2	.88	6.53	23.0	34.3	-.88	-.64
	s2	.22	1.62	.22	.07	-1.4	-.52	-1.65	-1.4	-.4	1.07	.05
	d_1	.62	1.15	.39	.67	21.7	.25	3.11	11.9	24.6	-.95	-.42
	d_2	.38	1.81	.98	1.78	52.6	-.66	.15	-4.9	27.3	.31	-.33
Oklahoma	s_1	.48	1.00	.42	.73	23.4	.98	6.64	19.1	32.8	----	-.85
	s2	.52	1.60	.24	.22	5.0	-.08	-.29	1.4	5.4	----	.72
	d_1	.40	1,03	.41	.60	18.9	.64	3.68	22.6	34.1	----	-2.28
	d_2	.60	1.99	.75	1.61	41.7	.24	1.27	3.4	31.1	----	-.97
Mean[3]	s_1	.74	1.03	.33	.70	25.8	1.23	6.14	22.6	36.4	-1.53	-1.58
	s_2	.26	1,81	.17	.14	5.3	.23	.06	2.7	5.8	.48	-.85
	d_1	.60	1.07	.30	.58	19.5	.64	2.81	14.0	24.9	-.89	-1.07
	d_2	.40	2.02	.59	1.05	30.9	.72	.78	2.4	21.2	.02	-.88

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[1] Selection differentials in this table for N_b, N_w, T_w, and $\overline{W}$ are one-half of the actual superiority of the dam's litter. Hence, Index = $4\left(N_b + 2N_w + \frac{T_w}{15}\right) + W_{154}$, for values of N_b, N_w and T_w in this table

[2] Including two additional lines of Polands for sow performance only, with 10 line-seasons and 148 litters.

[3] Each station mean was weighted by the number of line-seasons, omitting the Illinois "slow" line.

TABLE 4B -- ANNUAL SELECTION DIFFERENTIALS FOR ALL SIRES, ALL DAMS AND ALL PARENTS ($\Delta S, \Delta D$ AND ΔP)[4]

			Selection Differentials								
			Litter Size		Litter Wt. (lbs.)		Pig Wt. (lbs.)			Inbreeding %	
Station	Group	$\overline{A}$ (yrs.)	N_b	N_w	T_w	$\overline{W}$	W_{56}	W_{154}	Index	Dam	Litters
Illinois "Rapid"	ΔS	1.00	.32	.45	14.6	.48	4.97	24.1	32.7	.32	-.20
	ΔD	1.00	.40	.75	21.2	.29	2.88	10.3	23.5	-.03	-.04
	ΔP	1.00	.36	.60	17.9	.38	3.92	17.2	28.1	-.14	-.12
Illinois "Slow"	ΔS	1.22	.32	.84	18.0	-.86	-2.75	-28.1	-14.4	-.10	-.39
	ΔD	1.27	.15	.41	5.7	-.70	.39	-10.1	-4.6	.04	-.05
	ΔP	1.24	.24	.63	11.9	-.78	-1.18	-19.1	-9.5	-.03	-.22
Indiana	ΔS	1.50	.34	.62	27.3	1.38	4.54	19.7	33.4	-.96	-3.05
	ΔD	1.38	.33	.70	26.2	.78	2.21	10.8	17.5	-.66	-1.52
	ΔP	1.44	.34	.66	26.8	1.08	3.38	15.3	25.4	-.81	-2.28
Iowa	ΔS	1.23	.31	.63	23.2	1.25	4.68	18.1	30.5	-1.51	-1.74
	ΔD	1.47	.30	.63	20.6	1.09	2.17	11.7	23.4	-1.03	-.93
	ΔP	1.35	.30	.63	21.9	1.17	3.42	14.9	27.0	-1.27	-1.34
Missouri	ΔS	1.15	.25	.44	16.0	.69	4.87	20.7	29.6	-.39	-1.80
	ΔD	1.27	.29	.49	17.5	.72	2.56	10.4	20.3	-.07	-2.20
	ΔP	1.21	.27	.47	16.8	.70	3.72	15.5	25.0	-.23	-2.00
Nebraska	ΔS	1.17	.18	.45	18.6	.66	5.12	18.6	27.7	-.60	-.51
	ΔD	1.40	.54	.95	29.7	.09	2.81	9.7	27.4	-.79	-.44
	ΔP	1.29	.36	.70	24.2	.38	3.97	14.2	27.6	-.70	-.47
Oklahoma	ΔS	1.31	.34	.57	18.1	.65	4.56	14.1	24.9	-	-.03
	ΔD	1.61	.58	1.02	29.0	.55	3.12	17.4	35.6	-	-1.88
	ΔP	1.46	.46	.79	23.5	.60	3.84	15.8	30.2	-	-.96
Mean[3]	ΔS	1.22	.28	.56	20.8	.97	4.79	18.0	29.2	-1.11	-1.23
	ΔD	1.44	.39	.75	23.8	.73	2.49	11.8	25.6	-.85	-1.02
	ΔP	1.33	.34	.65	22.3	.85	3.64	14.9	27.4	-.98	-1.13

[4] $$\Delta P = \frac{\overbrace{s_1A_1^s+s_2(A_2^s-A_1^s)\,N_2^s}^{\Delta S(T)} + \overbrace{d_1A_1^d+d_2(A_2^d-A_1^d)\,N_2^d}^{\Delta D(T)}}{A_1^s+N_2^s(A_2^s-A_1^s) + A_1^d+N_2^d(A_2^d-A_1^d) = 2\,T}$$, where

A_1^s and A_1^d are mean ages of sires and dams respectively, selected as pigs; A_2^s and A_2^d are ages for those retained more than one season; and N_2^s and N_2^d are proportions of progeny from the older sires and dams, respectively. ΔS is the left half of the numerator divided by T, and ΔD is calculated similarly.

little additional emphasis is given to the information used in their selection as young boars. However, opportunity for selection among tried boars was slight (64 percent retained, Table 3) and most of the decisions were made before the boars' first progeny were weaned. Furthermore, it has been shown (Dickerson and Hazel, 1944b) that expected progress from selection for *average effects* of genes on rate of growth would not be increased by using older boars selected on the basis of progeny tests. Hence, it seems likely that use of fewer older sires in the developmnt of the inbred lines would have meant larger *annual* selection differentials for all sires ($\triangle$ S, Tables 4B and 5B).

Selection among older sows was greater than among gilts ($d_2 > d_1$ Table 4A) for litter size and for litter average weaning weights, largely because selection among sows could be based on their own rather than the dams' productivities, but also because the proportion retained in culling sows was only slightly greater than in culling of gilt pigs (48 and 33 percent, respectively). However, there was little additional culling of sows for their own growth rates or conformation scores as gilt pigs (Tables 4A and 5A). Hence, selection among sows for the index combining productivity and growth rate was slightly less than that among gilt pigs (Table 4A). These results were reasonably consistent among the five stations at which any older sows were used as breeders.

Comparison of sexes: Although opportunity for selection was much greater among boar pigs than among gilt pigs (i.e. 8 vs. 33 percent retained), the average selection for litter size at farrowing and weaning was little greater for boars (.33 and .70 pigs) than for gilts (.30 and .58 pigs). The greater opportunity for selection among boars was utilized mainly to emphasize individual weights at weaning (6.1 vs. 2.8 lbs.) with consequent greater emphasis on litter average weaning weights (1.2 vs. 0.6 lbs.), on total litter weight at weaning (26 vs. 20 lbs.) and on individual weights at 154 days of age (23 vs. 14 lbs.). Fine and Winters (1952) also found that selection for dam's litter size was greater, relative to opportunity, among gilts than among boar pigs (.48 vs. .74 pigs for number born and .88 vs. 1.07 pigs for number weaned, for two lines). In the present study, selection for the index combining sow productivity and growth rate was almost 50 percent greater for the boar than for the gilt pigs selected (36 vs. 25 units). Net selection of all sires was weaker than of all dams ($\triangle$ S and $\triangle$ D, Table 4B) for size of litters farrowed and weaned, due to the rather extreme emphasis on individual weaning weights of boar pigs and to the culling among older sows on the basis of their own litter performance. Consequently, net selection for the index

TABLE 5A -- ANNUAL SELECTION DIFFERENTIALS FOR SCORES OF CONFORMATION OF LIVE ANIMALS

Station and No. line-seasons	Age-sex	N	$\bar{A}$ (Yrs.)	Selection Differentials						
				Vigor etc.	Quality	Body Length	Details Conf.	Animal as Whole	Market Grade	Total Score
Illinois	s_1	1.00	1.00	.81	.54	.60	.77	.91	.92	4.51
"Rapid"	d_1	1.00	1.00	.39	.35	.26	.26	.37	.37	1.95
Hampshire 8	ΔP	1.00	1.00	.60	.44	.43	.51	.64	.64	3.23
Illinois	s_1	1.00	1.22	-1.32	-.78	-1.02	-.81	-1.13	-1.11	-6.29
"Slow"	d_1	1.00	1.27	-.24	-.15	-.18	-.39	-.34	-.40	-1.66
Hampshire 6	ΔP	1.00	1.24	-.78	-.47	-.60	-.60	-.74	-.76	-3.97
Iowa	s_1	.74	1.04	.44	.17	.29	.57	.53	.26	2.27
12 Poland	s_2	.26	1.95	.09	-.01	.12	.00	.11	.12	.45
lines	d_1	.70	1.05	.36	.12	.14	.32	.37	.35	1.66
89	d_2	.30	1.88	.15	-.01	.06	.10	.13	.14	.54
	ΔS	1.00	1.28	.36	.14	.24	.45	.44	.23	1.88
	ΔD	1.00	1.30	.32	.09	.12	.28	.36	.30	1.43
	ΔP	1.00	1.29	.34	.12	.18	.36	.40	.26	1.66
Missouri	s_1	.87	1.00	.28	.84	.57	.91	.67	.15	3.41
3 Poland	s_2	.13	1.94	1.05	-.55	-.15	-.59	-.21	.36	-.08
lines	d_1	.74	1.00	.52	.44	.31	.57	.97	.36	3.15
14	d_2	.26	1.97	.28	.32	.05	.28	.45	.17	1.54
	ΔS	1.00	1.12	.34	.66	.48	.74	.54	.18	2.92
	ΔD	1.00	1.25	.50	.42	.28	.54	.94	.32	3.00
	ΔP	1.00	1.18	.42	.54	.38	.64	.74	.25	2.96
Oklahoma	s_1	.46	1.00	.44	.42	.20	.52	.61	.39	2.59
3 Duroc	s_2	.54	1.64	.34	.19	.22	.11	.23	.34	1.45
line	d_1	.25	1.00	1.05	.80	.48	.79	1.08	1.06	5.28
38	d_2	.75	1.97	.16	.05	.10	.06	.14	.07	.54
	ΔS	1.00	1.34	.36	.32	.18	.36	.45	.33	2.01
	ΔD	1.00	1.73	.76	.54	.36	.54	.77	.72	3.69
	ΔP	1.00	1.54	.56	.43	.27	.45	.61	.53	2.85
Mean[1]	s_1		1.02	.41	.30	.29	.59	.57	.28	2.47
141	s_2		1.86	.25	-.01	.13	-.03	.11	.20	.67
	d_1		1.03	.56	.34	.25	.47	.62	.54	2.74
	d_2		1.91	.17	.04	.07	.11	.16	.12	.64
	ΔS		1.28	.36	.24	.25	.45	.45	.25	2.02
	ΔD		1.41	.46	.24	.20	.38	.53	.42	2.19
	ΔP		1.35	.41	.24	.22	.41	.49	.33	2.11

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[1] Omitting the Illinois lines because scores were given at a standard age instead of at a standard final weight; and weighting mean for each station by its number of line-seasons.

TABLE 5B -- ANNUAL SELECTION DIFFERENTIALS FOR DESCRIPTIVE SCORES OF LIVE ANIMALS

Station and No. Line-Seasons	Age-Sex	Head Jowl	Shoulder	Arch Back	Slope Rump	Leg Length	Depth Body	Ham Plumpness	Shape Back	Width Body
Illinois	s_1	.36	.31	.45	.38	.61	.73	1.03	.54	.77
"Rapid"	d_1	.21	.07	.11	.16	.30	.28	.37	.19	.22
8	ΔP	.28	.19	.28	.27	.45	.50	.70	.36	.49
"Slow"	s_1	-.20	-.32	-.27	-.46	-.64	-1.00	-1.05	-.39	-1.03
6	d_1	-.05	.06	-.27	-.03	-.44	-.39	-.29	-.10	-.18
	ΔP	-.12	-.13	-.27	-.24	-.54	-.69	-.67	-.24	-.60
Missouri	s_1	1.02	1.04	.15	.55	.44	.09	.78	.06	.49
3 Poland	s_2	.24	-1.20	-.25	.54	-.42	.61	1.50	.14	1.03
line	d_1	.26	.30	.08	.27	.12	.28	.21	.21	.32
14	d_2	.30	.38	.08	-.11	.14	.14	.11	.09	.36
	ΔS	.92	.80	.08	.56	.30	.19	.78	.08	.54
	ΔD	.28	.32	.10	.20	.12	.27	.20	.20	.32
	ΔP	.60	.56	.09	.38	.22	.23	.49	.14	.43
Oklahoma	s_1	.25	.15	.34	.34	.42	.17	.39	.27	.21
3 Duroc	s_2	-.11	-.04	-.28	-.05	-.04	.31	.22	.19	.26
line	d_1	-.15	.09	.08	.19	-.03	.49	.44	.45	.52
38	d_2	.02	.10	-.06	.29	.03	.06	.16	.14	.10
	ΔS	.14	.09	.16	.21	.26	.18	.30	.22	.18
	ΔD	-.09	.11	.02	.26	-.01	.35	.36	.36	.39
	ΔP	.03	.10	.09	.24	.13	.26	.33	.29	.29
Average[1]	s_1	.46	.39	.29	.80	.43	.15	.49	.21	.29
52	s_2	-.02	-.35	-.27	.11	-.14	.39	.56	.18	.47
	d_1	-.04	.15	.08	.21	.01	.43	.38	.39	.47
	d_2	.12	.18	-.02	.18	.06	.08	.15	.13	.17
	ΔS	.35	.28	.14	.30	.27	.18	.47	.18	.28
	ΔD	.01	.17	.04	.24	.02	.33	.32	.32	.37
	ΔP	.18	.22	.09	.27	.15	.25	.37	.25	.33

[1] Omitting the Illinois lines and weighting Oklahoma and Missouri by the number of line-seasons for each.

combining growth and sow productivity was little greater for all sires than for all dams.

Selection differentials for conformation scores at market weight averaged slightly larger for gilts than for boars (2.74 vs. 2.47 points, Table 5A), even though more than four times as many gilts were selected. This discrepancy was extreme at only one station and may have arisen because too much culling of boars was done at weaning age. However, earlier sexual maturity and ranting of the faster growing boars also may have lessened their apparent superiority in conformation at market weight, compared with all boars and barrows scored.

All parents: The average annual selection differentials for all age groups of parents in Tables 4B and 5B show definite positive selection for sow productivity, for growth rate, and for conformation. Of course, selection of all boars and of the gilt pigs for sow performance had to be based on the dam's litter rather than on their own performance. Hence, actual superiority in the dam's performance was twice as great as the figures given in Table 4A and 4B for litter size and litter weight. They are equivalent to selecting as boars and sows the pigs from dams whose gilt litters were above average by 2/3 of a pig (.54 to .92) in numbers farrowed, by 1 1/3 pigs (.94 to 1.58) in the numbers weaned, by 44 pounds (34 to 54) in total weight and by 1.70 pounds (.76 to 2.34) in average weight per pig at weaning. Fine and Winters (1952) found selection differentials of 1.2 and 1.94 pigs, respectively, for numbers born and weaned in the dam's litter. Superiority of selected parents amounted to 3.6 and 15 pounds in individual weight at 56 and at 154 days of age, respectively. Results were similar for the six stations (3.4 to 4.0 pounds for 56-day and 14.2 to 17.2 pounds for 154-day weights). Parents were 2.1 points above average in total score, ranging from 0.2 to 0.5 points above the mean for each of the six component scores. Part of this selection for superior conformation was undoubtedly due to the positive correlation of about 0.6 between 154-day weight and the score at market weight (Hazel, 1943) since selection favored longer, deeper, and wider bodies. In addition, there was selection for shorter legs, plumper hams, more level rumps, neater shoulders, trimmer jowls, and slightly higher arch of back. Rempel and Winters (1952) obtained a similar selection differential for 154-day weight (15.7 pounds) but a lower one for the total conformation score (.69 points compared to 2.1).

Selection for heterozygosity: There was a consistent and important tendency to select boar and gilt pigs from the dams and from the litters that were less highly inbred than the average (s_1 = —1.53 and —1.58 percent, d_1 = —.89 and —1.07, Table 4A). Also, in selecting older boars and sows to be used for a second or later season, the less highly inbred individuals were favored (s_2 = —.85, d_2 = —.88), but the dam's inbreeding no longer influenced selection among her adult progeny. This selection for greater heterozygosity is full of meaning because it was unintentional and indirect. It must mean that selection for superior performance of litters selects strongly for greater heterozygosity. Since much of the variation in performance of litters was due to non-genetic influences, a rather large part of the genetic variation must have been due to degree of inbreeding. Selection between litter mates could not have contributed to the observed selection for lower inbreeding, since calculated inbreeding is the same for full-sibs. However, actual degree of heterozygosity does vary among sibs, and selection of the better individuals within a litter could have contributed some additional selection for heterozygosity not measured by the inbreeding coefficient. Selection for greater heterozygosity would tend to maintain gene frequencies at intermediate values, and hence may help explain the limited effectiveness of selection within inbred lines.

Automatic and Deliberate Selection

By automatic selection is meant the selection that would occur because of differences in litter size, even if parents were chosen entirely at random from all individuals available at sexual maturity. Obviously, there is twice as much chance of saving an offspring for breeding from a litter of six as from a litter of three pigs weaned. Automatic selection differs from natural selection only to the extent that the size of litter in which an individual is reared influences the natural selective advantage of the individual in other respects. It seems highly unlikely that purely natural selection for larger litters could do more than maintain litter size, else nature would never arrive at an equilibrium for litter size. Hence, it is pertinent to know how much of the selection for larger litters was automatic.

Method

Automatic and deliberate selection among boar and gilt pigs for size and weight of the dam's litter were defined as follows:

Automatic = Mean per pig weaned less mean per litter farrowed.
Deliberate = Mean per pig selected less mean per pig weaned.
Net = Automatic plus deliberate.

Some of the stations computed automatic selection separately for boar and gilt pigs, although there appears to be no reason for expecting any sex difference other than from sampling variation except in the deliberate selection. For convenience, automatic selection is shown under both boars (B) and gilts (G) in Table 6.

TABLE 6 -- AUTOMATIC (A), DELIBERATE (D) AND NET (N) SELECTION AMONG BOAR (B) AND GILT (G) PIGS FOR PERFORMANCE OF THE DAM'S LITTER

Station and No. Line-Seasons	Type	Litter Size						Litter Weight Weaned (lbs.)					
		Born			Weaned			Total			Per Pig		
		B	G	All	B	G	All	B	G	All	B	G	All
Illinois “Rapid” 8	A	.70	.70	.70	1.48	1.48	1.48	33.2	33.2	33.2	-.41	-.41	-.41
	D	-.06	.10	.02	-.59	.03	-.28	-4.0	9.4	2.7	1.75	1.49	1.62
	N	.64	.80	.72	.89	1.51	1.20	29.2	42.5	35.9	1.34	1.08	1.21
Illinois “Slow” 6	A	.18	.18	.18	.94	.94	.94	18.8	18.8	18.8	-.36	-.36	-.36
	D	.48	.13	.30	.79	-.15	.32	17.9	-7.3	5.3	-1.06	-.63	-.84
	N	.66	.31	.48	1.73	.79	1.26	36.8	11.5	24.2	-1.41	-.99	-1.20
Indiana 13	A	.38	.37	.37	1.01	.95	.98	30.2	28.6	29.4	.12	.10	.11
	D	.59	.23	.41	.46	.44	.45	37.0	25.3	31.2	3.64	2.21	2.92
	N	.97	.60	.78	1.46	1.39	1.43	67.3	54.0	60.6	3.76	2.31	3.03
Iowa 202	A	.57	.57	.57	1.07	1.07	1.07	30.1	30.1	30.1	-.02	-.02	-.02
	D	.21	-.07	.07	.55	.12	.34	27.8	10.8	19.3	3.11	1.61	2.36
	N	.78	.50	.64	1.62	1.18	1.40	57.9	40.9	49.4	3.09	1.59	2.34
Missouri 32	A	.49	.47	.48	.88	.89	.89	21.9	21.8	21.8	-.55	-.45	-.50
	D	.05	-.12	-.04	.02	-.04	-.01	13.5	8.0	10.8	2.43	1.57	2.00
	N	.54	.35	.44	.90	.85	.88	35.4	29.8	32.6	1.88	1.12	1.50
Nebraska 95	A	.69	.68	.68	1.35	1.35	1.35	36.5	36.0	36.3	-.59	-.59	-.59
	D	-.31	.11	-.10	-.26	-.01	-.13	9.8	7.5	8.6	2.35	1.09	1.72
	N	.38	.78	.58	1.09	1.34	1.22	46.3	43.5	44.9	1.76	.50	1.13
Oklahoma 53	A	.84	.66	.76	1.10	1.11	1.10	26.1	26.0	26.1	-.21[1]	-.25[1]	-.25[1]
	D	0	.17	.08	.33	.07	.20	22.6	11.9	17.2	2.20[1]	1.53[1]	1.87[1]
	N	.84	.83	.84	1.43	1.18	1.30	48.7	37.9	43.3	1.95[1]	1.28[1]	1.62[1]
Wisconsin[2] 14	A	1.05	.82	.94	1.80	1.59	1.70	47.5	40.9	44.2	.38[1]	.04[1]	.21[1]
	D	-1.10	.22	-.44	-.16	.30	.07	18.3	17.6	18.0	2.98[1]	1.34[1]	2.16[1]
	N	-.05	1.04	.50	1.64	1.89	1.77	65.8	58.5	62.2	3.36[1]	1.38[1]	2.37[1]
Mean[3]	A	.64	.60	.62	1.15	1.15	1.15	31.1	30.7	30.9	-.21	-.21	-.21
	D	.02	.02	.02	.25	.09	.17	21.3	10.6	16.0	2.75	1.49	2.12
	N	.65	.62	.64	1.40	1.24	1.32	52.4	41.2	46.8	2.54	1.27	1.91

[1] Calculated indirectly from Automatic, Deliberate and Net selection for litter size and litter weight at weaning for these two stations.

[2] Selection among gilt pigs only during 3 line-seasons.

[3] Weighting each station mean by number of line-seasons, omitting Illinois “Slow”.

Results (Table 6)

The average results at the seven experiment stations indicate that if boar and gilt pigs had been selected at random, the superiority (*A* in the table) in size of the dam's litter automatically would have been nearly as great (i.e. .62 and 1.15 pigs, in numbers farrowed and weaned) as that actually obtained. The additional or deliberate selection (*D*, in the table) was nil for size of litter farrowed, slight for size of litter weaned (.25 pigs for boars and .09 pigs for gilts), but rather large for the litter average weaning weight per pig (2.75 pounds for boars and 1.49 pounds for gilts) and consequently for total litter weight (21.3 pounds for boars and 10.6 pounds for gilts).

Even though selection in the Illinois "Rapid" line was intended to be for rapid growth only, actual selection for litter size was essentially the same as at the six other stations where there was avowed emphasis on litter size, simply because selection for litter size was largely automatic. It is recognized that selection for superior individual growth and conformation without regard to size of litter might cancel at least a portion of the selection for larger litters, because of discrimination against the slightly smaller pigs usually found in the larger litters. This is suggested by the negative automatic selection for litter average weaning weight per pig (—.21 pounds). Further evidence is provided by the contrast between the Illinois "Rapid" and "Slow" lines in the indirect "deliberate" selection among boars for numbers weaned (—0.59 vs. 0.79 pigs) where deliberate selection presumably was solely for rapid and for slow growth rates, respectively. Apparently, the negative association between litter size and individual pig weights reduced somewhat the size of selection differentials for each, but particularly those for litter size.

Roughly, 27 percent of the total selection differential among boar and 40 percent of that among gilt pigs for the index combining growth and dam's productivity was due to the automatic selection for size of litter; the proportion was larger among gilts than among boars simply because there was less deliberate selection for growth rate among the gilts.

Potential and Actual Selection

Selection in Standard Deviation Units (Table 7 and Figure 1)

The extent to which opportunity for selection was utilized may be visualized most readily when the actual selection differentials for each trait and age-sex group of parents are divided by their standard deviations and thus are expressed in terms directly comparable with each other and with the potential maxima based on the proportion of the population retained. On this basis, automatic selection was twice as great for numbers weaned as for numbers farrowed, and each was

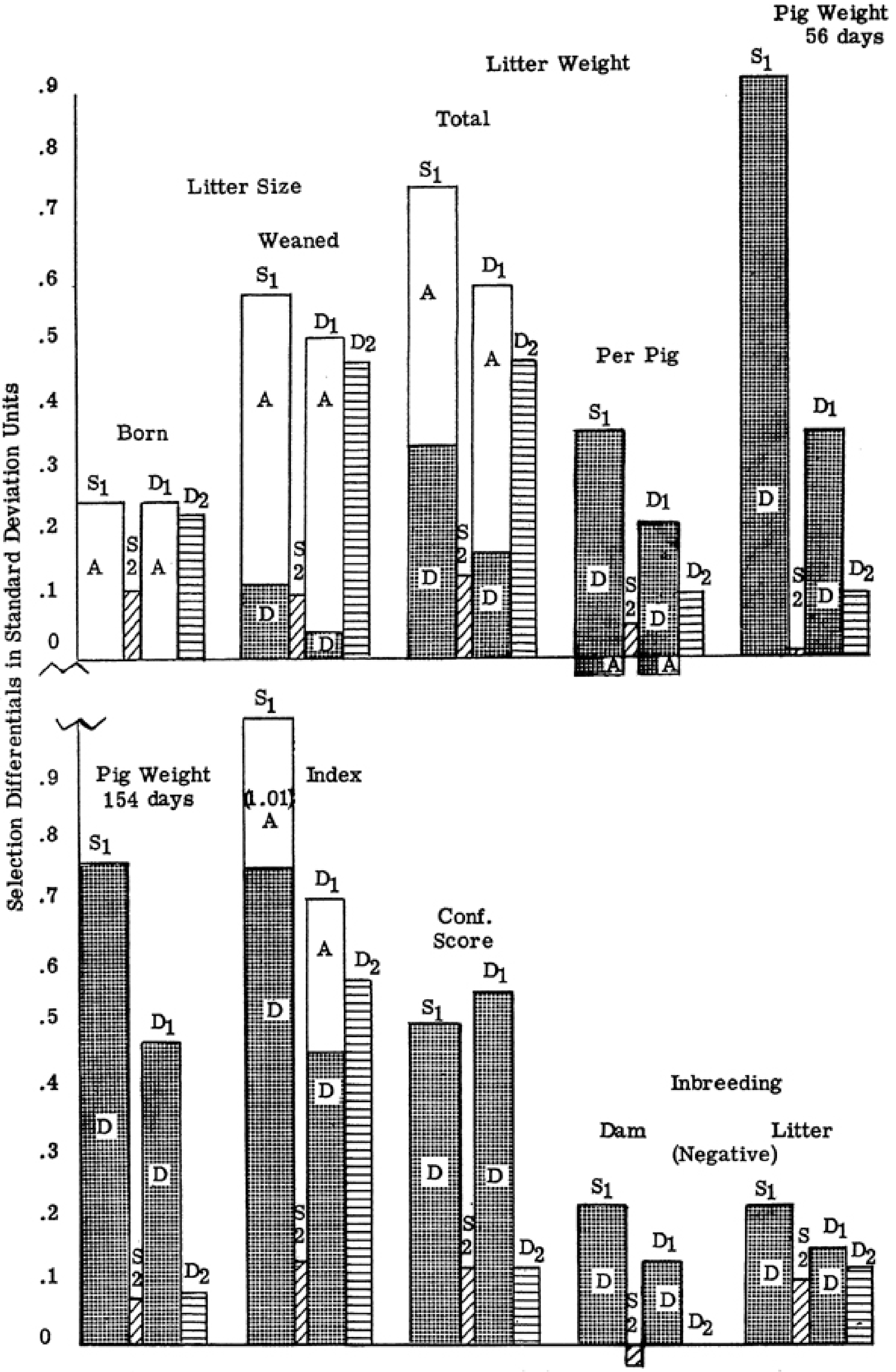

Figure 1. Graphic Portrayal of Automatic (A) and Deliberate (D) Selection Differentials in Standard Deviation Units for Ten Variables, by Ages and Sexes of Parents (from Table 7). (Width of columns is proportional to numbers of progeny weaned by parents of each age and sex).

TABLE 7 -- POTENTIAL AND ACTUAL SELECTION DIFFERENTIALS, IN STANDARD DEVIATIONS[1]

Among	Type sel.	Pot. max.	Litter size[2]		Litter wt.[2]		Pig wt.		Index	% Inbr.		Total conf. score
			N_b	N_w	T_w	$\overline{W}$	W_{56}	W_{154}		Dam	Indiv.	
All pigs	A	.52 (95)[3]	.24	.48	.44	-.03						
Boar pigs	D	1.74[4]	.01	.12	.34	.39	.92	.77	.76	-.22	-.22	.51
S_1	N	1.74	.25	.58	.75	.36			1.01			
Gilt pigs	D	1.05[4]	.01	.04	.17	.21	.38	.48	.45	-.13	-.15	.56
D_1	N	1.05	.24	.51	.59	.18			.71			
Older boars $S_2=s_2(A_2^s-A_1^s)$		.17[5]	.11	.10	.13	.05	.006	.07	.13	.05	-.10	.12
Older sows $D_2=d_2(A_2^d-A_1^d)$		.77(.41)[6]	.23	.47	.47	.10	.10	.08	.58	-.00	-.12	.12

[1] Using Table XX of Fisher and Yates (1938) in order to obtain expected superiority from truncation culling within unselected populations of the sizes actually weaned, as shown in Table 3.

[2] For the dams of gilt and boar pigs and of older boars, but for own performance of older sows.

[3] At birth and at weaning, respectively, assuming 68% survival of 11 fertilized ova to birth and 41% survival to weaning (i.e. .68(.60), since average survival of pigs born to weaning was 60% in these data (Squiers, et al. 1952).

[4] The potential maximum deliberate selection obtainable by reducing propulation from numbers weaned to numbers actually used as parents.

[5] From reducing numbers retained from 8.3% to 5.3% of those weaned.

[6] In parentheses, by reducing numbers retained from 33% to 16% of those weaned.

TABLE 8 -- PROPORTION SAVED IN TRUNCATION CULLING CORRESPONDING TO ACTUAL SELECTION DIFFERENTIALS IN TABLE 7.[1]

Among		Actual	Litter size		Litter wt.		Pig wt.		Index	% Inbr.		Total conf. score
			N_b	N_w	T_w	$\overline{W}$	W_{56}	W_{154}		Dam	Indiv.	
All pigs	A	.68 (.41) [2]	.86	.70	.73	.98						
Boar	D	.08	1.00	.94	.80	.77	.42	.50	.51	-.88	-.88	.68
pigs	N	.08	.86	.63	.52	.79			.36			
Gilt	D	.33	1.00	.99	.91	.89	.77	.70	.72	-.93	-.92	.65
pigs	N	.33	.86	.68	.62	.90			.54			
Older boars		.083 to .053										
Older sows		.48 or (.33 to .16)	.86	.69	.69	.94	.91	.93	.61	-.99	-.92	.81

[1] Using Table XX in Fisher and Yates (1938) for the average sizes of populations culled, as shown in Table 3.

[2] Proportions born and weaned, of 11 fertile ova per mating, based on 32 percent prenatal mortality of fertile ova and numbers born and weaned shown in Table 2A.

roughly half as great as that expected if all culling could have been based on that trait alone.

Opportunity for deliberate selection was utilized more fully for growth rate and for conformation than for size of litters. Individual weaning weight was the trait given most attention in selection of boars, followed by 154-day weight, conformation score, and litter average weaning weight, in that order. Among gilts, conformation score and 154-day weight received similar emphasis, with less attention to individual and litter average weaning weights. Deliberate but indirect selection for greater heterozygosity of both the litter and the dam was surprisingly large relative to that for index and for conformation, considering the presumed major role of non-genetic variation in performance. Net or total attention to the dam's litter performance was similar to that given weight at 154 days, but much of the net attention to litter performance was automatic in orgin, and hence its effectiveness is doubtful.

Opportunity for selection among tried boars was small, but most of it was used. Additional attention was given then to the index, to conformation at market weight, to the dam's litter performance, and to 154-day weight, in that order. There was nearly as much indirect emphasis on lower inbreeding among older boars as on their conformation or index as pigs.

Opportunity for selection among sows was much greater for own litter performance than for their earlier growth and conformation as gilts (i.e. .77 vs. .41 σ's). However, the actual selection among older sows, for early growth and conformation, was as great as that among tried boars, in addition to the heavy emphasis given to the sow's own litter performance. Lower inbreeding of the individual sows was given slightly more indirect emphasis than among tried boars, but received much less attention than did the sow's own litter performance.

Equivalent Truncation Culling (Table 8)

If selection could have been based entirely on one character, the proportion saved that would have the same average superiority as those actually selected is shown in Table 8, assuming approximately normal distribution. For example, although only 8 percent of the boar pigs were actually used as sires, the individual weaning weights of those used were representative of the heaviest 42 percent. Boars used were representative of the best 50 percent in 154-day weight and the best 68 percent in conformation, but were nearly typical of all boar pigs weaned in litter size of dam (100 percent for number farrowed and 94 percent for numbers weaned). Among gilts, the 33 percent actually selected were typical of the best 65 percent in conformation; 70 percent in 154-day weight, 77 percent in 56-day weight and 100 percent in dam's litter size. Inbreeding of the boar and gilt pigs selected, was typical of the lower 88 and 92 percent, respectively, of all pigs weaned, and the emphasis was nearly the same on inbreeding of the dams of selected pigs.

In selection among tried sows, 48 percent actually were retained, but these were representative of the best 69 percent in size and weight of litters weaned, the best 80 percent in gilt conformation score, and the 92 percent least inbred. The dam's inbreeding level had no influence on selection among their daughters as older sows. None would be expected if inbreeding of dams affected only the temporary maternal enviroment provided to the sows when they were suckling pigs.

Fraction of Potential Selection Applied (Table 9)

The proportion of the potential opportunity for *deliberate* selection that was utilized is computed by dividing the actual by the potential selection differentials. These fractions, given in Table 9, again show the relative emphasis given to different characters in selection, but their unique purpose is to show how much of the potential maximum *deliberate* selection differential was actually applied. The ideal measure of performance for this purpose would be an index (I) which included all of the characters considered, giving each the average emphasis it actually received. Such an index may be defined as follows:

$$I = \sigma_I \left[\frac{\beta_{IP \cdot WC}}{\sigma_P} (P) + \frac{\beta_{IW \cdot PC}}{\sigma_W} (W) + \frac{\beta_{IC \cdot PW}}{\sigma_C} (C) + \text{other factors} \right]$$

where P = dam's productivity index $= N_b + 2N_w + \frac{T_w}{15}$, W = 154-day weight and C = conformation score.

The relative weightings for each standard deviation of P, W and C (i.e. the β's) may be obtained from their actual selection differentials in standard deviation units, assuming that the correlation between W and C is 0.5 (Hazel, 1943 found $r = 0.6$) but that P is uncorrelated with W or C. For deliberate selection among *boar pigs* (Tables 4, 5 and 6);

$$\frac{\bar{s}_I}{\sigma_I} r_{IP} = \frac{\bar{s}_P}{\sigma_P} \text{ and } r_{IP} = \frac{(.02 + .50 + \frac{21.3}{15})}{9.45} \frac{\sigma_I}{\bar{s}_I} = .202 \frac{\sigma_I}{\bar{s}_I}$$

The estimate of $\sigma_P = 9.45$ comes from Table 2b where the index = 2 P + W and its standard deviation is 34.87 among pigs weaned in the same line and season.

TABLE 9 -- FRACTION OF POTENTIAL MAXIMUM SELECTION DIFFERENTIAL ACTUALLY APPLIED FOR EACH TRAIT (FROM TABLE 7)

Among		Litter size		Litter wt.		Pig wt.		Index[1]	% Inbreeding		Total conf. score
		N_b	N_w	T_w	$\bar{W}$	W_{56}	W_{154}		Dam	Indiv.	
All pigs	A	.46	.52	.47	-.03						
Boar pigs	D	.01	.07	.20	.22	.53	.44	.44	-.13	-.13	.29
	N	.14	.33	.43	.21			.58			
Gilt pigs	D	.01	.04	.16	.20	.36	.46	.43	-.12	-.14	.53
	N	.23	.49	.56	.17			.66			
Older boars		.64	.60	.78	.30	.04	.42	.76	.30	-.56	.68
Older sows		.30	.61	.61	.13	.24	.19	.75	-.01	-.29	.28

[1] See footnote 1, Table 4A.

$$\text{Hence, } \sigma_P = \sqrt{\frac{V\,(2\,P + W) - V\,(W)}{4}} = \sqrt{\frac{(34.87)^2 - (29.33)^2}{4}} = 9.45$$

$$\text{Similarly, } r_{IW} = \frac{22.6}{29.3}\,\frac{\sigma_I}{\bar{s}_I} = .771\,\frac{\sigma_I}{\bar{s}_I}, \text{ and } r_{IC} = \frac{2.47}{4.87}\,\frac{\sigma_I}{\bar{s}_I} = .507\,\frac{\sigma_I}{\bar{s}_I}.$$

Values for the standard partial regressions of I on P, W and C are derived from the above correlations, as follows:

$$r_{IP} = \beta_{IP \cdot WC} = .202\,\frac{\sigma_I}{\bar{s}_I}$$

$$r_{IW} = \beta_{IW \cdot PC} + .5\,\beta_{IC \cdot PW} = .771\,\frac{\sigma_I}{\bar{s}_I}$$

$$r_{IC} = .5\,\beta_{IW \cdot PC} + \beta_{IC \cdot PW} = .507\,\frac{\sigma_I}{\bar{s}_I}$$

Solution of the last two equations yields:

$$\beta_{IW \cdot PC} = .690\,\frac{\sigma_I}{\bar{s}_I} \text{ and } \beta_{IC \cdot WP} = .162\,\frac{\sigma_I}{\bar{s}_I}$$

It follows that the index actually employed for selecting boars on P, W and C was something like:

$$I = \left[\frac{.202}{9.45}\,P + \frac{.690}{29.3}\,W + \frac{.162}{4.87}\,C\right]\sigma_I = (.0214\,P + .0236\,W + .0333C)\,\sigma_I \text{ or relatively } I = P + 1.10\,W + 1.56\,C$$

$$\text{Hence, } \sigma^2_I = (9.45)^2 + (1.10)^2\,(29.3)^2 + (1.56)^2\,(4.87)^2 + 2(.5)\,(1.10)\,(29.3)\,(1.56)\,(4.87) = 1434,$$

And, $\sigma_I = 37.87$.

Selection *deliberately* applied for this index was:

$$\bar{s}_I = 1\,(1.94) + 1.10\,(22.6) + 1.56\,(2.47) = 30.65, \text{ or } .81\,\sigma_I$$

The selection differential for this index combining P, W and C, therefore, was only $\frac{.81}{1.74}$ or 46 percent as large as if all selection could have been based upon it, and corresponds to selecting boars representative of the best 48 percent of those weaned, instead of only the best 8 percent. The comparable index combining P, W and C for selection among gilt pigs was:

$$I = P + .88\,W + 8.73\,C, \text{ with } \sigma_I = 60.51$$

The deliberate selection differential for gilts was:

$$\overline{s}_I = (.02 + .18 + \frac{10.6}{15}) + (.88)\ (14.0) + (8.73)\ (2.74) = 37.15, \text{ or } .61\ \sigma_I$$

This is only 58.5 percent (i.e. $\frac{.61}{1.05}$) as large as the potential maximum and corresponds to selecting gilts representative of the best 61 percent in the index combining P, W and C, instead of the best 33 percent.

Comparison of these "indexes in retrospect" that, consciously or otherwise, were employed in the average *deliberate* selection, with the estimated optimum index of I = 2 P + W (Dickerson and Hazel, 1944a) indicates that the dam's productivity (P) actually received about one-half as much attention as most estimates of its economic importance and heritability appeared to warrant. Conformation score received relatively more positive attention in selection than seems justified (Hazel, 1943), particularly among gilts. These estimates of the actual relative emphasis given to P, W and C, of course, represent an average for all stations, years, and lines. Thus the weighting actually used for any *particular* year and line could have deviated greatly from the *average* index weighting.

Factors other than P, W and C accounted for nearly one-half of the culling among gilts [i.e. 46 percent, since $\underline{.54}$ (.61) = .33, the proportion actually selected] and for much more than half of that among boar pigs [i.e. 83 percent, since $\underline{.17}$ (.48) = .08]. Selection of boar pigs for individual weaning weights was 53 percent of maximum, more than for the index combining, P, W, and C. This undoubtedly was due to heavy culling (castration) at weaning time, and accounts in larger measure for the relatively poorer use of opportunity for selection among boars than among gilts, particularly for conformation score. Other factors which were responsible for some culling not measured in this investigation are hernias, cryptorchids, undesirable conformation not fully reflected in the score, post-weaning losses from diseases or injuries, discrimination against pigs from the younger litters and reproductive failures.

EFFECTIVENESS OF SELECTION

It is evident that a considerable amount of selection has been practiced during the development of many mildly inbred lines of swine. This selection has been based largely on the performance of individual animals within these lines, but some attention also has been given to merit of full-sibs. The effectiveness of such selection must be gauged by its ability to improve the average phenotypic effects of the genes carried by a line. This can be estimated from (1) the time trends in performance of the lines, adjusted for any decline due to increased inbreeding, and (2) from comparison of linecrosses and topcrosses with purebreds representative of the foundation stocks of the lines.

Time trends in performance can be misleading as measures of genetic change because they may be influenced by time trends in nutrition, disease, management, climate, or other non-genetic factors. Also, estimates of the decline in performance associated with the reduced heterozygosity resulting from inbreeding are subject to sampling error. Nevertheless, when based on large numbers of lines over long periods of time, such adjusted time trends constitute important evidence concerning the effectiveness of selection. Data suitable for study of inbreeding effects and of time trends in performance of the lines were available from the Iowa, Minnesota, Nebraska, and Oklahoma stations. These data were analyzed and the results are given on the following pages. Preliminary results of these analyses have been reported earlier (Dickerson *et al.*, 1947; Kottman, *et al.*, 1948; Dickerson, 1951, 1952).

Reports from rather extensive tests of boars from inbred lines (Hazel, *et al.*, 1948; Durham, *et al.*, 1952) in comparison with non-inbred boars of the same breed in two-sire herds on Iowa and Wisconsin farms, have indicated no average superiority for the inbred boars, but have provided evidence of line differences and of an important degree of heterosis when stocks of diverse genetic origin were crossed. Results reported by Chambers and Whatley (1951) from Oklahoma do suggest that crossing of selected lines within a breed may accomplish significant improvement over non-inbred stock of the same breed.

Influence of Inbreeding on Performance

Effects of inbreeding on performance of the lines themselves can be estimated (1) by comparing linecrosses with parental lines of known inbreeding and relationship (pedigree) within the same season of farrowing, and (2) from the linear regression of performance on the inbreeding coefficient among the unselected progeny within the same line and season. Estimates obtained from intra-season comparisons of lines with their crosses ordinarily will have smaller sampling errors than those from regression within line and season, because of the much larger differences in level of inbreeding upon which the former are based. Also, the inferiority in performance of inbred lines compared with their crosses measures *directly* the cumulative effect on performance of the inbreeding practiced, since the performance of crosses among unrelated lines is influenced by changes in gene frequencies resulting from selection but not by the inbreeding of the lines (except for maternal effects of inbred dams). Because selection unintentionally favored the less inbred litters, we may assume that it also tended to favor the more heterozygous individuals among those having the same calculated degree of inbreeding. Thus the *actual* decline in heterozygosity over several generations would be smaller than indicated by the inbreeding coefficient. Likewise, the actual decline in performance per unit of rise in the inbreeding coefficient would tend to be smaller than that estimated from regression of performance on inbreeding coefficient within lines and seasons (as in studies by Fine and Winters, 1952, 1953, and by Rempel and Winters, 1952).

Ideally, to measure inbreeding effects (1) crosses should be compared with their parent lines for the same lines (and with the same weighting of each) that are used to measure the time trends in performance, (2) each group of lines crossed should have been derived from the same non-inbred foundation stock, in order to avoid including effects of crossing unrelated strains in the estimates of inbreeding decline within strains, and (3) the same degree of selection should have been practiced in choosing the inbred parents of the inbred and linecrossed litters.

These conditions were most nearly fulfilled in the Iowa data, since all twelve lines of Poland China were maintained throughout the period studied and eight of the twelve lines were derived either wholly or in part from a single foundation herd. The fact that each of four of the lines were unrelated to any of the other lines would tend to cause intraline inbreeding effects to be overestimated from linecrossing results. The Nebraska Duroc lines also were related, but relationship between lines was less at Minnesota and Oklahoma.

To the extent that inbred parents (particularly dams) used to produce inbred litters were more highly selected than those used to produce linecrosses, inbreeding effects would tend to be underestimated from comparison of inbred and linecrossed litters. Similar bias would result if the more vigorous inbred lines tended to be represented more heavily than the weaker lines in the linecross-inbred comparisons. This bias would be partially offset by correspondingly fewer degrees of freedom for time trends of the lines that were discontinued because they did not withstand inbreeding well.

Inbreeding of the litter affects performance of the pigs directly through their genetic constitution, whereas the inbreeding of the dam affects only the maternal environment provided for the pigs.

Inbreeding of the Litter (Tables 10, 11, 12)

Effects of the litter inbreeding were estimated from paired comparisons of inbred and linecross litters from sows of the same line, farrowed during the same season and under the same herd management. The amount and suitability of the data are shown in Table 10.

TABLE 10 -- DATA FOR COMPARISON OF INBREDS (I) AND LINECROSSES (C) WITHIN SEASON AND LINE OF DAM

Station and Breed	Kind of Mating	Number of				Mean		
		Seasons	Season-lines of Dam	Lines or Crosses	Litters	Age of Dams (mo.)	Inbreeding % of Dams	Inbreeding % of Litters
Nebr. Durocs	C	7	22	18	78	13.4	23.3	7.0
	I			8	167	18.7	20.5	27.7
Okla. Durocs	C	10	22	15	89	18.5	21.4	0.3
	I			6	131	20.2	19.9	22.7
Minn. Poland Chinas	C	5	11	9	49	16.2	36.2	5.2
	I			6	123	17.5	36.1	41.7
Iowa Poland Chinas	C	4	31	57	109	14.2	32.3	4.0
	I			11	117	19.4	30.4	37.2
Total	C	26	86	99	325			
	I			31	538			

TABLE 11 -- MEAN SUPERIORITY OF CROSSES OVER INBREDS, WITHIN SEASON AND LINE OF DAM[1], ADJUSTED TO ZERO DIFFERENCE IN AGE OF DAM AT FARROWING

	Regression	Actual Mean (C-I)				(C-I) Adjusted for Age[2]					
	on Age	Durocs		Polands		Durocs		Polands		Wtd.	Std.
Variable	in Months[2]	Nebr.	Okla.	Minn.	Iowa	Nebr.	Okla.	Minn.	Iowa	Mean	Error[3]
Litter size (pigs)											
Farrowed	.243	-.68	-.094	.339	-.557	.61	.30	.65	.70	.56	± .24
At 21 days	.126	.62	.747	.429	.197	1.29	.95	.79	.85	1.01	± .20
At 56 days	.135	.70	.867	.720	.313	1.42	1.09	.89	1.01	1.13	± .18
At 154 days	.139	.80	1.131	.894	.444	1.53	1.36	1.07	1.16	1.31	± .21
Pig weight (lbs.)											
At birth	.000	-.04	.03	-.05	-.18	-.04	.03	-.05	-.18	-.06	± .06
At 21 days	.036	-.51	.31	-.55	-.66	-.30	.38	-.45	-.50	-.17	± .23
At 56 days	.153	-2.99	.67	.14	-.23	-2.11	.94	.23	.46	-.22	± .69
At 154 days	.600	3.5	8.9	9.9	8.9	7.0	10.1	10.3	11.7	9.6	± 3.10
Age of dam (mos.)		-5.3	-1.6	-1.3	-5.2	0	0	0	0	0	
% inbreeding:											
Dams		2.8	1.4	0.2	1.8	2.8	1.4	0.2	1.8	1.7	
Litters		-20.7	-22.4	-36.5	-33.3	-20.7	-22.4	-36.5	-33.3	-27.4	

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[1] The mean difference from each season and line of dam was weighted in proportion to the reciprocal of its error variance,

$$w = \frac{n_C \cdot n_I}{n_C + n_I},$$ where n_C and n_I are numbers of observations for crosses and inbred, respectively.

[2] The linear regression of performance on age of dam, for the 59 degrees of freedom between lines within station and season, was used to adjust the mean difference in performance to zero difference in age of dam.

[3] Based on the fact that the F ratio from Table 12 equals t^2 and that the standard error of the weighted mean difference equals:

$$\frac{\text{Mean difference}}{\sqrt{\text{F Ratio}}}$$

TABLE 12 -- VARIANCE ANALYSIS OF WEIGHTED[1] MEAN DIFFERENCES (CROSS MINUS INBRED) WITHIN LINE OF DAM AND SEASON, ADJUSTED FOR REGRESSION ON AGE OF DAM

Source of Variation	Degrees of Freedom	Adjusted Mean Square							
		Litter Size at Age in Days				Pig Weight in Lbs. at Age in Days			
		0	21	56	154	0	21	56	154
Inbr. (C-I)	1	31.51*	85.70**	125.92**	168.58**	2.673	12.76	24.7	40258.**
Inbr. x station	3	1.26	3.79	2.05	1.70	2.436	29.96	398.7	775.
Inbr. x season within station	22	9.40*	7.63**	6.73**	4.78	2.503	27.05	151.0	3561.
Inbr. x line of dam within season and station	59	5.52	3.43	3.05	4.42	2.460	22.67	239.4	4226.

*Means $P \leq .05$; ** means $P \leq .01$

[1] See footnote 1, Table 11.

The mean difference, crosses minus inbreds, was calculated for each of the 86 subclasses for season and line of dam. Note that percentage of inbreeding averaged 20.7 to 36.5 lower for crosses than for inbreds at the four stations, whereas the differences in the dam's inbreeding were negligible by comparison. The dams of the inbred litters doubtless were somewhat more highly selected than those used for crossing since the former were used in perpetuating and in attempting to improve lines. This would tend to make conservative the estimates of inbreeding effects derived from these comparisons. Dams of the inbred litters also were older, particularly at Nebraska and Iowa. To remove any bias and experimental error arising from variation in age of dam, the differences in performance were adjusted to zero mean difference in age of dam, using the estimates of regression obtained from the 59 degrees of freedom between lines within season and station. These regression coefficients and both the actual and the adjusted mean differences are given in Table 11.

Notice that after the adjustment to zero mean difference in age of dam, the estimates of inbreeding effect on litter size and 154-day weight were consistently large at all four stations and highly significant.

The analysis of variance in Table 12 indicates that differences between stations in the total inbreeding decline were of minor importance, if differences in the level of inbreeding are ignored. However, the total inbreeding decline for the more highly inbred Poland lines at Iowa and Minnesota was smaller in litter size and little more in 154-day weight than for the less highly inbred Duroc lines at Nebraska and Oklahoma. Differences in the heterosis or crossing effects on litter size, between seasons at the same station, were large enough for significance but could have been due partly to the steady rise of inbreeding from year to year.

Roughly one-half of the decline in litter size associated with inbreeding of the litter was due to increased pre-natal mortality, since linecrossed and inbred litters both were produced by inbred sows of the same lines. Most of the remainder was due to deaths before the pigs were weaned. In proportion to the mean for the crosses, inbreeding decline was nearly three times as great in viability as in weight of survivors at 154 days of age.

The estimates of inbreeding decline at the four stations are expressed in more comparable terms as decline per 10 percent of inbreeding in Table 14. The major station difference was the greater inbreeding effect on post-natal mortality among the Duroc lines. However, the estimated effect of 10 percent inbreeding of *litter* used by Fine and Winters (1952) in their study of Minnesota data was —.28 pigs for number farrowed (ex Comstock and Winters, 1944) and —.83 pigs for number weaned, based on regression of performance on inbreeding within season and line.

The latter is based on data from one line of crossbred foundation and is nearly four times as large as the estimate obtained in the present study from the Minnesota comparisons of linecrossed and inbred litters representing the same lines of Poland China.

The major effect of pig's own inbreeding on viability and its lesser influence on growth rate have been demonstrated in the earlier studies of Comstock and Winters (1944), Dickerson, *et al.* (1946), Sierk and Winters (1951), Chambers and Whatley (1951), Hetzer, *et al.* (1951), and others.

Inbreeding of the Dam (Table 13)

Data for estimating the effect of the dam's inbreeding upon litter performance from comparison of 3-line and 2-line crosses were available for two seasons at the Iowa station (Table 13). The 3-linecross litters were from 2-linecross dams which averaged 34.2 lower in percentage of

TABLE 13 -- COMPARISON OF 3-LINE AND 2-LINE CROSSES WITHIN SEASON AND LINE OF SIRE

A. Data Used

Station and Breeding	Kind of Mating	Number of			
		Seasons	Seasons-lines of Sire	Inbred Lines	Litters
Iowa Poland China	3-line cr.	2	20	12	63
	2-line cr.			12	50

B. Mean Superiority of 3-Line over 2-Line Crosses

Variable	3-Line less 2-Line		Mean for 3-Line crosses
	Actual	Adjusted	
Litter size at:			
Birth	.53 ± .35	.59	6.74
21 days	.96 ± .30	1.06	5.06
56 days	.76 ± .28	.87	4.53
154 days	.84 ± .30	.96	4.24
Pig weight (lbs.) at:			
Birth	.20	.20	2.91
21 days	.40	.38	9.8
56 days	-.18	-.19	27.1
154 days	-.55	.45	116.7
Age of dam (mos.)	.03	.03	11.72
Inbreeding %			
Dams	-34.2	-34.2	2.68
Litters	2.9	0	4.04

C. Variance Analysis

Source of Variable	D/F	Mean Squares for Litter Size at			
		0	21	56	154
Inbreeding of dam	1	7.61	24.31**	15.42*	18.64**
Season	1	.63	.12	1.93	5.92
Line of sire within season	18	3.34	2.48	2.17	2.36

* Signifies $P \leq .05$; ** that $P \leq .01$.

inbreeding than did the dams of the 2-linecross litters, but there was little difference in either inbreeding of litters or in age of dams. Inbreeding of the dams was found to cause an important and highly significant decline in litter size, ranging from 0.53 pigs at birth to 0.96 pigs at 21 days. These results suggest that the inbred dams were inferior in suckling ability, as well as in ovulation rate or in prenatal nourishment of the young. At birth and at 21 days, weights of pigs from the inbred dams were smaller, but not significantly so, and there were no demonstrable effects on pig weights at 56 and 154 days. These differences are in the same direction, but are smaller than those reported by Chambers and Whatley (1951) for Durocs.

When adjusted to zero difference in litter inbreeding, the advantage of the 3-linecross litters was increased somewhat. Again, for a more effective comparison the influence of the dam's inbreeding is expressed in Table 14 as change in performance per 10 percent increased inbreeding of dam. Expressed in the same manner, the estimates obtained by Chambers and Whatley (1951) for effects of inbreeding of dam among Durocs are roughly twice as large as those shown in Table 14 for Poland China (i.e. —.56, —.48, —.50 and —.69 for live pigs per litter at 0, 21, 56, and 154 days of age, respectively; and —2.18 pounds for 154-day weight per pig. These Duroc lines were unrelated in orgin, however, and hence may include linecrossing effects not properly to be considered as *intra-line* inbreeding effects.

Inbreeding of a Line (Table 14)

The effect of inbreeding level on the performance of the line itself contains the effects of both the litters' and the dams' inbreeding. It could be estimated by comparing 3-linecross with inbred litters, which amounts to summation of the separate effect from inbreeding of litters and of dams, as shown in Table 14. These are conservative estimates of the inbreeding handicap on performance of the lines themselves. Yet, these estimates indicate that long continued inbreeding would mean virtual extinction of these lines of swine, provided that the decline in performance is linearly associated with inbreeding level, and unless it is ameliorated by selection accompanying the inbreeding and by important differences between lines in rate of inbreeding decline. Fine and Winters (1952) used an estimated decline of 0.37 pigs farrowed and 1.3 pigs weaned per litter for each rise of 10 percent inbreeding of a line, based on regression within line and season, in contrast with the estimated decline of 0.35 and 0.49 pigs based on comparison of linecrosses with the parental inbred lines that were used in the present study (i.e. 0.24 pigs from litter inbreeding plus 0.25 pigs from dam's inbreeding, Table 14).

TABLE 14 -- CHANGE IN PERFORMANCE FOR EACH 10 PERCENT INBREEDING FROM INTRA-SEASON COMPARISON OF LINECROSSES AND PARENTAL INBRED LINES

Inbreeding of:	Breed	Station	Litter Size at Ages				Pig Wt. (lbs.) at Ages			
			0	21	56	154	0	21	56	154
Litters (Adjusted to zero difference in age of dam)	Poland	Iowa	-.21	-.26	-.30	-.35	.05	.15	-.14	-3.50
	China	Minn	-.18	-.22	-.24	-.29	.01	.12	-.06	-2.82
	Duroc	Nebr.	-.30	-.62	-.69	-.74	.02	.15	1.02	-3.37
		Okla.	-.14	-.43	-.49	-.61	-.01	-.17	-.42	-4.49
	Mean1/		-.20*	-.35**	-.38**	-.44**	.02	.08	.03	-3.44**
			±.08	±.07	±.06	±.07	±.021	±.085	±.25	±1.11
Dams (Adjusted to zero difference in litter inbreeding)	Poland China	Iowa	-.17.	-.31**	-.25*	-.28**	-.06	-.11	.06	- .13
			±.12	±.10	±.10	±.10				
Litters plus Dams	All	All	-.38	-.65	-.63	-.72	-.03	-.03	.08	-3.57
		Iowa	-.38	-.56	-.56	-.63	-.00	.04	-.08	-3.64

* signifies that $P \leq .05$; ** that $P \leq .01$.

1/ Weighting the mean difference for each station in proportion to the inverse of its error variance (i.e. according to

$$v_i = \frac{(\Sigma w_i)\, I^2}{100}, \text{ where } w_i = \frac{n_I \cdot n_C}{n_I + n_C}$$

for a season and line of dam within a station, and I = weighted mean difference (C-I) in percentage of inbreeding for a station.

Similarly, Fine and Winters (1953) used estimated declines for 10 percent inbreeding in 154-day weight per pig of 6.6 and 13.4 pounds, compared with the estimate of 2.95 pounds based upon intra-year comparison of crosses with parent lines of Poland China (Table 14) used for all Minnesota data in the present study. The larger absolute inbreeding effects assumed by Fine and Winters probably are partially justified because their study was limited to two lines derived from crossbred foundation stock, with consequent greater heterozygosity and higher level of performance at the same calculated level of inbreeding, compared with the lines developed within the Poland China breed.

Time-Trends in Performance Within Lines

The two genetic determinants of time-trends in performance within lines which are subject to some control by the breeder are changes (1) in gene frequencies $(\overline{q})$, and (2) in degree of heterozygosity (f). If selection is able to increase gradually the frequencies of favorable alleles, the difference between crosses and parent lines *per unit of inbreeding* (f) should diminish, since inbreeding effect is proportional to $\underline{2kq\,(1-q)\,f}$ and $\underline{q}\,(1-\underline{q})$ decreases as $\underline{q}$ becomes either larger or smaller than 0.5. If there is no heterozygote advantage (i.e. if $k \leqq 1$), such selection should improve performance of crosses among the inbred lines in proportion to $2q[1+k\,(1-q)]$, slightly, while performance of the inbred lines declines curvilinearly as $2q[1+k\,(1-q)\,(1-f)]$. In addition to the effects of any change in gene frequency (q) from selection, performance of crosses would be expected to exceed that of the non-inbred foundation stock because of the increased heterozygosity of crosses between unrelated stocks. Under these circumstances, the decline in performance of inbred lines under inbreeding and selection would be smaller than the difference in performance between the inbred lines and their crosses.

By contrast, if heterozygote advantage $(k \overline{>} 1)$ were important, increasing $\underline{q}$ above the "equilibrium" value of $\frac{(1+k)}{2k}$ through selection within inbred lines would tend to gradually *lower* the performance level of crosses a little. Hence, the decline in performance with advancing generations would be less likely to be smaller than the difference in performance between the resulting inbred lines and their crosses. Evidence that selection within inbred lines of swine failed to improve, or depressed, performance of crosses among the lines would seem to mean either (1) that little or no change in gene frequencies had occurred in response to selection or (2) that selection had increased frequencies of the more favorable alleles and had thus prevented part of the inbreeding decline to be expected without selection, but that performance of crosses among the lines "stalled" or declined because of heterozygote superiority ($k > 1$) for many loci. Failure of the decline in performance with advancing inbreeding within lines to depart noticeably from linearity would seem to indicate that selection had made no major change in gene frequencies (i.e. if change in $\underline{2kq(1-q)(1-f)}$ is linearly associated with $\underline{f}$).

Intra-Line Regression on Inbreeding

The linear regressions of litter size and pig weights at each age on the average inbreeding of the litter, between seasons within lines, are shown in Table 15, for data from each of four cooperating stations. A total of 46 lines, with an average of 8 to 10 seasons for each, are represented.

It is evident that the actual declines in litter size averaged as large as, and that declines in pig weight at 56 and 154 days of age were larger than, the recovery in performance obtained by crossing unrelated lines. Of course, it is entirely possible that an adverse trend in exposure to disease or parasites may have contributed to the unexpectedly rapid decline in growth rates at some of the stations.

This approach is subject to the criticism that part of the inbreeding variation between seasons within a line sometimes represented a fluctuation resulting from an alternating between close inbreeding within sublines and the crossing of such sublines, as well as a systematic upward trend. Such fluctuations in level of inbreeding between adjacent seasons would be similar in nature to those between inbred lines and their crosses and hence do not provide a wholly independent estimate of inbreeding effects.

Linear Time-Trends in Performance and Inbreeding

The pooled intra-line regressions of performance and of litter inbreeding on years are shown in Table 16 for five stations. The average declines per year were 0.15, 0.16 and 0.21 pigs, respectively, in size of litters at birth, 21 and 56 days of age, and were 0, 0.19, 0.35, and 4.0 pounds for pig weights at birth, 21, 56, and 154 days of age, respectively. Contrary to the expectations based on estimates of heritability and of inbreeding effects (Comstock and Winters, 1944), selection was unable to offset inbreeding effects for growth rate any more than for litter size.

The average yearly increase in calculated inbreeding ranged from 2.3 at Oklahoma to about 3.9 percent at Nebraska and Missouri, with intermediate rates of inbreeding rise at Minnesota and Iowa (2.6 and 3.4 percent, respectively). In general, rates of decline in both litter size and pig weight were more severe at the stations where the lines were inbred more rapidly.

The rates of decline in performance items with increasing percentage of inbreeding ($\triangle_{XF}$) shown in Table 16 were those estimated independ-

TABLE 15 -- LINEAR TREND IN PERFORMANCE PER 10 PERCENT OF INBREEDING, BETWEEN SEASONS WITHIN LINES

Station Breed	Number of Lines	Number of Line-Seasons	Litter Size at Ages 0	21	56	154	Pig Wt. (lbs.) at Ages 0	21	56	154
Iowa Poland	12	115	-.52	-.54	-.68	-.79	-.02	-.54	-1.95	-5.44
Minn. Poland Crosslines	14[3] 2[3]	104[3] 22[3]	-.79	-.31	-1.23	----	-.02	.04	- .59	[2]
Nebr. Duroc	11	85	-.63	-.42	-.60	-.83	-.03	-.33	-1.71	-14.79
Okla. Duroc	7	77	-.32	-.43	-.50	-.71	-.06	-.08	- .18	-6.51
Recovery from crossing[1]	Iowa		-.38	-.56	-.56	-.63	-.00	.04	- .08	-3.64
	All Stations		-.38	-.66	-.63	-.72	-.03	-.03	.08	-3.57

[1] Litter plus dam inbreeding effects, from Table 14.

[2] Omitted because of incomplete data.

[3] Fewer for data at 21 days of age.

ently from intraseason comparison of inbred lines and their crosses (see Table 14). The expected yearly decline from inbreeding rise alone is obtained by multiplying annual inbreeding rise by the rate of inbreeding decline in performance (i.e. $b_{FT} \triangle_{PF}$). Subtracting the expected yearly *decline* from increased homozygosis from the actual time-trend in performance provides an estimate of the time-trend freed from inbreeding effects (i.e. $b_{XT} - \triangle_{XF} b_{FT}$). To obtain estimates of the effective heritability of variation in litter size and growth rate, the adjusted time-trend in a given trait need only be divided by the corresponding annual selection differential for all parents (Table 4b).

The adjusted time-trends (b'_{XT} in Table 16) give little evidence that selection was effective during the development of these inbred lines. There was no average positive trend in litter size and the adjusted trends in pig weight were rather consistently negative. Improvement most nearly fulfilled expectations at the Oklahoma station where inbreeding was least intense and where greatest use was made of older sires and dams (i.e. 0.18 pigs per year in numbers weaned compared with a selection differential of 0.80 pigs, and a loss of only 0.6 pounds per year in 154-day weight). On the basis of deliberate selection practiced and published estimates of heritability, little improvement in the size of litters but an *annual* gain in 154-day weight of roughly 2 pounds would be expected [i.e. 15 (.2) —3.4 (.36)], after correction for inbreeding effects. If the estimates of inbreeding effect were too small, because of either sampling error or use of second choice inbred parents to produce the crosses (Table 10), or if adverse time-trends in exposure to disease or parasites were operative, the adjusted time-trends may be more pessimistic than is justified.

If the larger estimates of dam's inbreeding effects obtained by Chambers and Whatley (1951) for Oklahoma Duroc lines had been used to remove inbreeding effects from the time-trends in Duroc lines at Nebraska and Oklahoma (Table 16), their corrected trends in litter size would have been —.08 and 0.17 pigs at birth, 0.19 and 0.23 pigs at 21 days and 0.03 and 0.24 pigs at 56 days, respectively. These estimates of yearly change are larger by 0.06 to 0.09 pigs per litter weaned than those used. The mean trend for all stations, however, would still be only slightly positive (about 0.04 pigs per year), although perhaps as large as was to be expected from the small amount of *deliberate* selection for larger litters and the presumed low degree of determination by average gene effects. Similar substitution of Chambers' and Whatley's (1951) larger estimate of dam's inbreeding effect on 154-day weight would change the corrected yearly trend only to —6.10 pounds at Nebraska and —.15 pounds at Oklahoma.

The apparent contradiction between these results for litter size and those reported from the Minnesota station by Fine and Winters (1952) and by Rempel and Winters (1952) vanishes if the estimates of inbreeding effect based on intra-season comparison of linecrosses and parental inbred lines are used to correct their time trends. For example, the actual linear changes per year for the two lines studied by Fine and Winters were —.037 and —.183 for number farrowed, —.260 and —.155 for number weaned, and 3.2 and 3.1 for percent of inbreeding. Using —.035 and —.050 (from Minnesota and Iowa data, Table 14) as rates of inbreeding decline for numbers farrowed and weaned, the time trends adjusted to zero, change in inbreeding become 0.075 and —.075 pigs, averaging zero for number born; and —.10 and 0.00, averaging —.05 pigs for number weaned. The real time-trend, with inbreeding effects removed, probably was intermediate between these estimates and those reported by Fine and Winters, since larger absolute effects of inbreeding would be expected in these lines derived from crossbred foundation because of their greater initial heterozygosity and higher levels of performance.

TABLE 16A--LINEAR CHANGE PER YEAR WITHIN LINES FOR ACTUAL PERFORMANCE (b_{XT}), INBREEDING (b_{FT}), AND PERFORMANCE ADJUSTED FOR INBREEDING (b'_{XT})

A. Litter Size

Character (X)	Station	D/F	b_{XT}	b_{FT}	Δ_{XF}[1]	b'_{XT}[3]	No. of lines	Breeds
Litter size at birth	Iowa	103	-.167	3.43	-.0382	-.036	12	Poland
	Minn.	110	-.086	2.61	-.0351	+.006	2 14	Crossline Poland
	Nebr.	74	-.411	3.84	-.0470	-.231	11	Duroc
	Okla.	70	+.008	2.26	-.0309	.078	7	Duroc
	Mo.	27	-.050	3.87	(-.0366)[2]	.092	2 1	Poland Hamp.
	Mean	384	-.151			-.032	49	
Litter size at 21 days	Iowa	103	-.185	3.43	-.0564	.008	12	Poland
	Minn.	60	-.270	4.85	-.0526	-.015	1 11	Crossline Poland
	Nebr.	58	-.219	3.73	-.0932	.129	11	Duroc
	Okla.	70	.029	2.26	-.0734	.195	7	Duroc
	Mean	291	-.158			.072		
Litter size at 56 days	Iowa	103	-.347	3.43	-.0557	-.156	12	Poland
	Minn.	104	-.134	2.80	-.0499	+.006	2 11	Crossline Poland
	Nebr.	74	-.427	3.84	-.0940	-.066	11	Duroc
	Okla.	70	.017	2.26	-.0739	.184	7	Duroc
	Mo.	27	.057	3.87	(-.0529)[2]	.262	3	2 Poland 1 Hamp
	Mean	378	-.208			-.001		

[1] Taken from intra-season comparison of inbreds and crosses in Table 14.

[2] Unweighted mean of the Iowa and Minnesota estimates.

[3] $b'_{XT} = b_{XT} - \Delta_{XF} \cdot b_{FT}$

TABLE 16B -- PIG WEIGHTS

Character	Station	No. of lines	D/F	b_{XT}	b_{FT}	Δ_{XF}[1]	b'_{XT}[3]
Pig weight (lbs.) at birth	Iowa	12	103	-.009	3.43	-.00031	-.008
	Minn.	16	110	.014	2.61	-.00439	.025
	Nebr.	11	74	-.018	3.84	-.00708	.010
	Okla.	7	70	.006	2.26	-.00355	.014
	Mean		357	-.001			.015
Pig weight (lbs.) at 21 days	Iowa	12	103	-.341	3.43	.00403	-.354
	Minn.	12	63	-.358	3.69	.00134	-.363
	Nebr.	11	58	-.060	3.73	.00376	-.074
	Okla.	7	69	.094	2.02	-.02787	.150
	Mean		293	-.186			-.182
Pig weight (lbs.) at 56 days	Iowa	12	103	-.730	3.43	-.00837	-.701
	Minn.	13	107	-.022	2.57	-.00068	-.020
	Nebr.	11	74	-.937	3.84	+.10743	-1.35
	Okla.	7	69	.268	2.02	-.03647	.342
	Mo.	3	27	-.112	3.87	(-.00453)[2]	-.094
	Mean		380	-.346			-.403
Pig weight (lbs.) at 154 days	Iowa	12	103	-2.166	3.43	-.36366	-.917
	Minn.[4]	13					
	Nebr.	11	74	-8.227	3.84	-.35046	-6.880
	Okla.	7	69	-1.494	2.02	-.46186	-0.559
	Mo.	3	27	-5.611	3.79	(-.32931)[2]	-4.363
	Mean		273	-3.980			-2.784

[1] Taken from intra-season comparison of inbreds and crosses in Table 14.
[2] Unweighted mean of the Iowa and Minnesota estimates.
[3] $b'_{XT} = b_{XT} - \Delta_{XF} \cdot b_{FT}$
[4] Omitting Minnesota, because of incomplete data for 154-day weights.

The results reported by Rempel and Winters (1952) for 8 lines of Poland Chinas also indicated greater effectiveness of selection than those shown in Table 16 for 14 lines of Poland Chinas and 2 of crossbred foundation from the same station. Again, the major cause of the discrepancy was that Rempel and Winters used an estimated decline of 1.3 pigs weaned per litter (data from one line of crossbred foundation) and 6.8 pounds in 154-day weight per pig (Whatley, 1942; Iowa Poland China data) for each increase of 10 percent inbreeding of the line, based on regression within season and line, whereas in the present study corresponding declines of 0.50 pigs and 2.95 pounds were used, based on comparison of Minnesota Poland China linecrosses with their parental inbred lines, but using the Iowa data to estimate dam's inbreeding effects. To the extent that calculated inbreeding over-estimates the actual reduction in degree of heterozygosity through many generations of selection and mild inbreeding, use of the regression of performance on inbreeding within season and line overestimates the actual inbreeding effect on the time trend in performance. The estimates of inbreeding effect based on comparisons of linecrosses with inbred lines would not be subject to this bias, as discussed earlier. Another difference was that all 14 Poland lines were included in the present analysis to avoid any selection between lines. Even when all lines are included, the lines that were discarded sooner because of unsatisfactory performance are represented during fewer seasons, and the weighted average time-trend is likely to be more favorable than would have been the case if no lines had been discarded.

Constancy and Linearity of Inbreeding Depression

It is sometimes maintained that inbreeding affects some lines more adversely than others. The data from 12 lines of Poland China swine during 9 years at the Iowa station provide some interesting information concerning line differences in response to inbreeding. The intra-line regressions of actual yearly means for 154-day litter size, pig weight, and litter weight on the change in litter inbreeding over the 9-year period are shown in Table 17A. Note that the regressions of litter size, pig weight and total litter weight on inbreeding were negative in all 12 of the lines, with one lone exception (0.01 for Line B in pig weight). Line differences in rate of inbreeding decline were remarkably small for litter size and for total weight of the litters but were relatively large for pig weight at 154 days.

TABLE 17A -- REGRESSION OF UNADJUSTED 154-DAY LITTER PERFORMANCE ON INBREEDING OF LITTER, BETWEEN YEARS WITHIN LINES, FOR 12 IOWA LINES

	Regressions on Inbreeding Percentage			
Line	Litter Size	Pig Weight lbs.	Litter Weight lbs.	Mean % Inbreeding of Litters
A	-.066	- .63	-12.3	24.4
B	-.096	.01	-12.9	23.0
C	-.099	-1.53	-17.9	33.1
D	-.064	- .71	- 9.9	31.4
E	-.040	-1.45	- 9.0	49.8
F	-.064	- .16	- 8.8	32.8
G	-.133	- .56	-19.6	37.2
H	-.095	-1.18	-15.2	40.4
I	-.074	- .12	- 9.9	43.5
J	-.047	- .64	- 8.1	50.7
K	-.075	- .16	- 9.9	39.1
S	-.086	- .57	-12.8	28.8
Mean	-.079	- .63	-12.3	36.2
% change1/	-1.65	-0.44	- 1.84	

1/ Relative to the mean at 20 percent inbreeding of litters. See Fig. 2.

The analysis of variance in Table 17B, indicates that line deviations in the regression on inbreeding were highly significant for pig weight at 154 days, but were even smaller than expected from sampling error alone for litter size and litter weight at 154 days. The average regressions

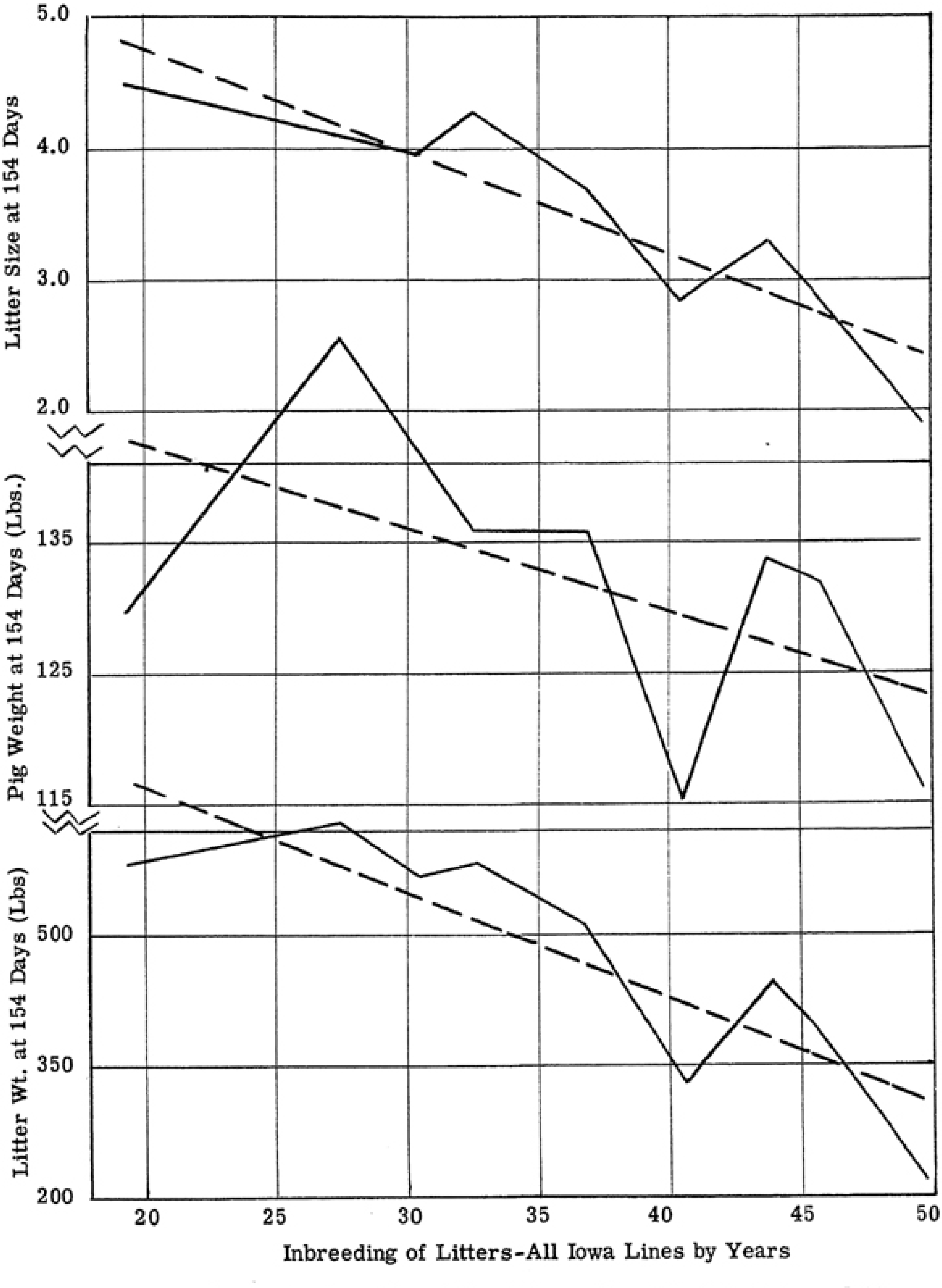

Figure 2. Change in Actual 154-Day Litter Size, Pig Weight and Litter Weight with Advancing Inbreeding of Litters During Nine Years for Twelve Lines of Poland China Swine at the Iowa Station.

TABLE 17B -- ANALYSIS OF VARIANCE IN UNADJUSTED YEARLY AVERAGES FOR LITTER SIZE AND GROWTH RATE AT 154 DAYS OF AGE AMONG 12 IOWA LINES

Source of Variation	Degrees of Freedom		154-Day	
		Litter Size (Pigs)	Pig Weight (lbs.)	Litter Weight (lbs.)
Lines	11	3.395**	305**	73,457**
Years	8	8.489**	1516**	226,664**
Regression on Inbreeding	1	56.074**	3525**	1,358,925**
Remainder	7	1.691*	1234**	64,913**
Years x Lines	87	0.691	89	14,970
Line dev. in Regression on Inbreeding	11	0.468	198**	11,215
Remainder	76	0.724	73	15,513

** $P \leq .01$, * $P \leq .05$

on inbreeding were highly significant for litter size, pig weight, and litter weight. Yearly variation, in addition to that linearly associated with inbreeding, was significant but relatively unimportant for litter size, but was highly significant and large for pig weights, with litter weight intermediate in this respect.

Inspection of the trend in yearly averages (equal weight to each line mean) plotted against litter inbreeding, in Figure 2, suggests no systematic departure from a linear decline. The linearity of the inbreeding decline and the relatively small line differences in rate of decline both are in harmony with the expectation based on dominance for large numbers of genes with small individual efforts. The highly significant line differences in average performance levels may be attributed to the known large line differences in mean inbreeding levels and the presumed differences in gene frequencies, and are not in conflict with essentially similar rates of decline for all lines. However, the highly significant line differences in rate of inbreeding decline for 154-day weight suggest that smaller numbers of genes are involved for individual growth rates than for prolificacy and viability.

FACTORS LIMITING EFFECTIVENESS OF SELECTION

Selection is effective to the extent that the selected parents transmit genes whose average effects are superior to the mean of their generation. This effective heritability of parental superiority in phenotype is limited by variation due both to uncontrolled environmental variation and to dominance and epistasis which cause genetic deviations from average gene effects. Also, genetic and environmental correlations between components of total performance may reduce progress from selection sharply, even though heritability remains relatively high for each of the components.

Correlations Between Characters

Genetic and environmental correlations between the component traits (X_i) of total performance (I) affect both the size of the selection differentials obtained ($\bar{s}_I$) and the extent to which they represent genetic superiority (i.e., their effective heritability, b_{GI}). The general principles can be illustrated best with the admittedly artificial example of selection for *n* traits, assuming variation in each to be equally important and heritable, and that each trait is correlated equally with all other traits (i.e., $r_{G_1G_2} = r_{G_1G_3}$ etc., $r_{E_1E_2} = r_{E_1E_3}$ etc.). The superiority in I of selected parents for any given proportion retained is directly dependent on the variability in the index, (σI). Now if $I = X_1 + X_2 + \cdot \cdot + X_n$ and $r_{x_ix_j}$ is the average correlation between any two components of the index, then

$$\sigma I = \sqrt{n \cdot V\ (X)\ [1 + (n - 1)\ r_{x_ix_j}]}\ \cdot \qquad (4)$$

Whether genetic or environmental, positive correlation between any pair of component traits expands, and negative correlation contracts, the average size of selection differentials for each component (i.e.,

$$\bar{s}_{x_i} = \bar{s}\frac{\sigma I}{n} = \bar{s}\,\bar{\sigma}_{x_i}\sqrt{\frac{1 + (n - 1)\ r_{x_ix_j}}{n}}$$

). Relative to selection differentials when $r_{x_ix_j} = \underline{0}$, the limits are $\sqrt{n}$ times as large when $r_{x_ix_j} = 1$ and 0 when $r_{x_ix_j} = \frac{-1}{(n-1)}$.

Expected improvement from selection usually has been computed as the product of the selection differential and the heritability ($\bar{s}_{x_1}b_{G_1x_1}$) for each trait separately, ignoring the fact that both the natural and the deliberate selection actually applied must be based on some sort of an index combining a number of correlated traits. The possible discrepancy between (1) the heritability applicable to the selection differential actually obtained for a single trait when selected is based on an index, $I = \Sigma_n X_i$ and (2) the estimate from regression of offspring on parent or from sib-correlations for that trait, may be clarified by examining the ratio of (1) to (2) as follows:

$$\frac{b_{G_1x_1} \text{ when selection on } I = (\Sigma_n X_i)}{b_{G_1x_1} \text{ estimated for } X_1 \text{ alone}} =$$

$$\frac{n \cdot V(G_1)\ [1 + (n - 1)\ r_{GG}]}{n \cdot V(X_1)\ [1 + (n - 1)\ r_{XX}]} \cdot \frac{V(X_1)}{V(G_1)} = \frac{[1 + (n - 1)\ r_{GG}]}{[1 + (n - 1)\ r_{XX}]} \qquad (5)$$

Clearly, any tendency for the environmental (and hence the gross) correlation between traits to differ in the positive direction from the genetic correlation would make effective heritability less than that estimated for individual traits. Also, the effective heritability of selection for total performance would decline toward zero if negative genetic correlation between traits approached $\frac{-1}{(n-1)}$ in size. If the number of component traits is even moderately large, very small negative genetic correlations will sharply reduce effective heritability compared with that estimated for the individual traits (e.g., if $n = 5$, $r_{GG} = -.25$ would reduce effective heritability to zero).

It seems quite likely that favorable environmental influences on the general health of an individual animal will benefit, and that detrimental environmental factors will injure, several of the traits included in total performance, particularly those expressed during the same stage of development (Wright, 1922). This would introduce positive environmental correlations between traits that would tend to cancel any negative genetic correlations, giving intermediate values for the gross correlations between traits. Analyses of the genetic and enviromental correlations between components of performance in swine have been too sketchy to know yet whether they will provide an adequate explanation for the apparent ineffectiveness of the selection actually applied in the developmnt of the inbred lines of swine studied. Negative genetic correlations between suckling ability and efficiency in gaining ability and between rapid gains and desirable (leaner) carcasses have been indicated (Dickerson, 1947). Also, the slightly negative gross correlation between the pig's 154-day weight and its dam's productivity (Hazel, 1943) may consist of positive environmental and negative genetic correlation. Positive environmental correlations between traits expressed during *different* periods of life are less likely to be important, as shown by Hazel *et al.* (1943) in swine and by Krueger *et al.* (1952) in chickens.

Attempts to avoid the consequences of genetic and environmental correlation by selecting for one trait at a time appear to be quite futile. The ratio of expected improvement in all *n* traits ($\triangle G_t$) from selection based on total performance (I) to that from selection based on one trait alone (X_i) is:

$$\frac{\triangle G_t \text{ from } \overline{s_I}}{\triangle G_t \text{ from } \overline{s_{X_i}}} = \frac{\sigma_I}{\sigma X_i} \cdot \frac{n \cdot V(G)\,[1+(n-1)\,r_{GG}]}{n \cdot V(X)\,[1+(n-1)\,r_{XX}]}$$

$$\frac{V(X)}{V(G)\,[1+(n-1)\,r_{GG}]} = \sqrt{\frac{n}{1+(n-1)\,r_{XX}}}, \qquad (6)$$

since the net effect of selection for one trait alone is the sum of its effects on all n traits. The factor, other than n (Hazel and Lush, 1942), which determines the relative effectiveness of index and single trait selection is the size of the gross correlation between traits (r_{XX}). Index selection is less than $\sqrt{n}$ times as effective when r_{XX} is positive; the two methods approach equal effectiveness only as $r_{XX} \rightarrow 1.0$. Index selection would be more than $\sqrt{n}$ times as effective as single trait selection when r_{XX} is negative and the advantage approaches infinity as $r_{XX} \rightarrow \frac{-1}{(n-1)}$. Negative change in genetic correlation with no change in phenotypic correlation would reduce the effectiveness of index and single trait selection in exactly the same proportion, in terms of the change in all n traits. However, negative genetic correlation is likely to make the phenotypic correlation smaller or more negative, and hence to increase the advantage of index selection.

Dominance and Epistasis

Some degree of dominance is the most likely genetic mechanism by which change in heterozygosity, from inbreeding or crossbreeding, would affect performance levels. Expected decline is proportional to $2\ k\ F\ q\ (1-q)$, where k is degree of dominance (Hull, 1945, 1952) defined in terms of phenotypic scale as (2 Aa-AA-aa) / (AA-aa). F is Wright's inbreeding coefficient, and q is frequency of the preferred dominant allele. The effectiveness of selection within inbred lines in preventing part of the decline in performance from inbreeding and in improving the performance of crosses between inbred lines is expected to be greatest when the number of segregating chromosomal units is small, when the degree of dominance is low, and when the rate of inbreeding is slow. In the present experiment, rate of inbreeding was moderate, but the number of loci obviously was large.

Crow (1952) has suggested (1) that when the number of loci is large, selection is likely to be relatively powerless to prevent inbreeding depression from fixation of the recessive alleles, even though rate of inbreeding is slow, and (2) that if selection within (or between) inbred lines is able to reduce frequency of unfavorable, completely recessive alleles below their equilibrium levels in the non-inbred foundation stock and thus prevent part of the inbreeding depression, it still would not improve performance of linecrosses appreciably (i.e., performance of crosses is proportional to $2q\ (2-q)$ when $k = 1$, for complete dominance, as noted on page 44). However, the type of gene interaction that most surely would produce inbreeding deterioration relatively unresponsive to selection and no improvement in cross performance is heterozygote advantage.

On the scale of dominance, heterozygote superiority corresponds to $k > 1$, since k describes superiority of the heterozygote relative to that of the more favorable homozygote. Here each allele (or chromosome segment) may be visualized as having some partially or completely dominant favorable effects not possessed by other alleles at the same locus. A heterozygote is assumed to be superior to either alternative homozygote by virtue of its greater number of favorable gene effects.[3]

At such loci, selection within non-inbred populations would move gene frequencies toward some intermediate equilibrium values. Total genetic variability would be great, but only a small part would be due to the average effects of genes, making selection relatively ineffective. Inbreeding depression from dominance [i.e., $2\ k\ F\ q_A\ (1 - q_A)$] would be severe, not only because k is large but also because $q_A\ (1 - q_A)$ would be large when q_A remains at an intermediate value.

The recent critical and extensive study by Cockerham (1952) indicated that within inbred lines of swine at the Iowa station, estimated heritability from regression of progeny on dam was zero or slightly negative for litter size and not significantly positive for growth rate. Earlier studies had indicated higher heritabilities for both litter size (e.g. Lush and Molln, 1942; Stewart, 1945; Cummings, *et al.,* 1947; Blunn and Baker, 1949) and rate of growth (e.g. Whatley, 1942; Baker, *et al.,* 1943; Krider, *et al.,* 1946). Cockerham's results conformed rather closely to those expected if heterozygote advantage were important for both litter size and growth rate without requiring much negative genetic correlation between these two complex traits. The higher level of inbreeding and the statistical elimination of differences between age group of dams in Cockrham's data may account in part for his lower estimates of heritability.

The fact that the time-trends, after removal of inbreeding effects, averaged zero for litter size and negative for growth rate (Table 16) certainly indicates a high degree of dominance and probably heterozygote advantage (i.e., $k > 1$) for some of the loci which control these traits. If loci without overdominance (simple recessives) account for most of the depressing effects of inbreeding (Crow, 1952), more critical demonstration of the importance of heterozygote advantage may need to await results from selection experiments designed to produce maximum hetero-

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[3] An alternative hypothesis, that the heterozygote is superior merely because it is intermediate, corresponds to epistasis without dominance of primary gene effects, with an optimum genetic intermediate giving maximum performance. When approach to the optimum intermediate is governed by genes at several loci, some of the homozygous genotypes are intermediate and selection should be able to reduce fixation of the more extreme homozygotes under mild inbreeding, as in the case of partial to complete dominance.

zygosity in crosses between complementary strains (Dickerson, 1952). However, the recent demonstrations of the selective advantage of heterozygotes at certain loci which control cellular antigens of blood in chickens (Briles and McGibbon, 1948; Briles, 1949; and Shultz and Briles, 1953) add to the evidence for heterozygote superiority.

Most examples of epistasis or gene interaction include dominance. *Without dominance* of *primary* gene effects, inbreeding decline appears likely only from epistasis in which selective advantage for a given gene may range from positive to negative, depending upon the other genes present in a given individual. In this instance, a decline in performance would be expected because of the increased average deviation from the optimum genetic intermediate (as in the model used by Wright, 1935) among individuals in a population of inbred lines. This sort of inbreeding depression is expected to be somewhat curvilinear, (i.e. decline at an ever decreasing rate with advancing inbreeding), compared with the linear and potentially extreme decline expected from dominance of consistently favorable *primary* gene effects. Also, selection should be able to guide fixation of intermediate genotypes, thus tempering inbreeding decline.

However, in a balanced genetic system involving preferred intermediates for *n* different functions, the inbreeding depression could be severe and the deviation from linearity of inbreeding effects might not be readily detectable. It would be more difficult to explain how the rather consistently favorable effects from crossbreeding (Dickerson, 1952) could result from such a system of balanced epistasis, whereas varying degrees of dominance could account for both inbreeding and crossbreeding effects.

Evidence concerning the types of genetic variability which underlie important economic traits of swine is considered in greater detail elsewhere (Dickerson, 1952).

Variation in Heterozygosity

The fact that selection for superior performance resulted, indirectly, in choosing breeders from the less inbred litters and dams, (i.e., —1.58 and —1.53 percent for boar pigs; —1.07 and —.89 percent for gilt pigs, Table 4A) indicates that an important part of the variability in over-all performance was due to litter and to dam differences in heterozygosity. The correlation of the average index *(I)*, that apparently was used in deliberate selection, with inbreeding of litter (F_l) and of dam (F_d) can be estimated from the *deliberate* selection differentials for *I* in standard deviation units (Table 7), assuming that there was no selection directly for lower or higher levels of inbreeding, from the relation:

$$r_{IF_l} = \frac{\overline{s}_{F_l}}{\overline{s}_I} = \frac{-.226}{.81} = -.28 \text{ for boar pigs.}$$

"Deliberate" selection for index was used because only the "deliberate" selection was calculated for inbreeding of dam and litter. If there was any attention given directly to inbreeding *per se*, it was likely to have favored the more highly inbred pigs, and hence would tend to minimize the estimates obtained for r_{IF}. This approach yields estimates of r_{IF_i} = —.28 and —.25 and of r_{IF_d} = —.27 and —.21, for boar and gilt pigs, respectively. Apparently, 4 to 8 percent of the variance in pig indexes was linearly associated with inbreeding of litter or of dam. Together, inbreeding of litter and of dam would account for more nearly 8 to 12 percent of the index variance, because the correlation between F_i and F_d was not high, possibly 0.3. Also, variation in calculated inbreeding does not include the intra-litter variation in proportion of loci heterozygous, so that the association of performance with actual degree of heterozygosity must be still closer than with calculated inbreeding. The fraction of the variance due to inbreeding would be much less for any single trait such as growth rate, because much of the association with overall merit is due to the fact that inbreeding tends to have adverse and hence correlated affects on many different aspects of performance.

Intra-line varation in performance due to level of inbreeding limits the effectiveness of selection to the same degree as would a similar amount of variation from environmental influences, assuming that inbreeding level or the proportion of loci heterozygous in any individual is essentially independent of its *average* gene frequency. This would mean that the heritability or effectiveness of selection for the index would be reduced by only 8 to 12 percent because of the individual and family variability in proportion of loci heterozygous.

Other effects of choosing parents with calculated inbreeding 1.0 to 1.5 percent lower than the mean for their generation would be to retard the calculated rate of inbreeding below that intended, and further, to make the actual reduction in heterozygosity less than that indicated by the calculated inbreeding.

METHODS FOR INCREASING EFFECTIVENESS OF SELECTION

There is little doubt that the amount of selection applied for litter size, growth rate, and conformation during the development of the inbred lines studied here could have been increased by the following means:

1. More strict adherence to a predetermined index weighting of each character to increase deliberate selection for larger litters.
2. Less extreme culling of boars (by castration) for individual weights at weaning, in order to increase opportunity for selection based on

post-weaning growth rate and conformation. (Dickerson and Hazel, 1944a).

3. Adjustment of litter and individual performance records for variation in level of inbreeding of the dam and litter and in age of gilts at first farrowing (Stewart, 1946a).

However, there is doubt that such increases in amount of selection would have changed the effectiveness of selection materially. It seems more likely that the relative ineffectiveness of the selection that was applied can be attributed to the nature of the genetic and environmental variability in the characters under selection.

An approach that offers theoretical promise is direct selection for maximum performance of crosses between complementary strains, based on progeny tests of individuals and families in test-cross matings. Variations of this approach have been considered by Hull (1945, 1952) and by Comstock, *et al* (1949) for the improvement of corn, and by Dickerson (1952) for use in swine.

SUMMARY AND CONCLUSIONS

A cooperative study has been made of the amount and effectiveness of selection applied during the development of inbred lines of swine at several of the experiment stations participating in the Regional Swine Breeding Laboratory. Data used to measure intensity of selection included 4,521 litters from 38 lines during the period 1932 to 1948. Litter size and weight were adjusted to a first litter basis. Inbreeding level averaged 24 percent for all litters, and increased at the rate of 2 to 4 percent per year within lines. Conclusions with respect to the amount of selection applied and its effectiveness are as follows:

1. Young boars sired 74 and gilts produced 60 percent of the pigs weaned; the remainder were from older tried boars and sows. The generation interval or mean age of parents was 1.22 for sires and 1.44 for dams.
2. Opportunity for culling should have been greater among the 30 boars than among the 27 gilts weaned per line and season since only 8 percent of the boars but 33 percent of the gilts weaned were used to produce litters at one year of age. Older breeders represented 63 percent of the boars and 48 percent of the sows used the preceding season.
3. Superiority of young boars and gilts selected was similar for size of the dam's litter at birth (0.66 *vs.* 0.60 pigs) and at weaning (1.40 *vs.* 1.16 pigs), but superiority of boars was greater for individual weight at weaning (6.1 *vs.* 2.8 lbs.) and consequently for litter average weanling pig weight (1.2 *vs.* 0.6 lbs.), for total weaning weight of the

dam's litter (26 *vs.* 20 lbs.), for individual weight at 154 days of age (23 *vs.* 14 lbs.), for the index combining dam's productivity with individual weight at 154 days (36 *vs.* 25 units), and for inbreeding of the individual (—1.6 *vs.* —1.1 percent) and its dam (—1.5 *vs.* —0.9 percent). Superiority in total score of conformation at market weight was even slightly greater for gilts than for boar pigs (2.7 *vs.* 2.5 points).

4. Superiority of older boars retained over all boars used the preceding season was slight for dam's litter size, own growth rate and conformation, but again the less inbred individuals were saved (—.85 percent). Older sows that were retained surpassed all sows farrowing the previous season by 0.6 and 1.1 pigs in size of litters farrowed and weaned, by —.88 percent inbreeding but by only 2.4 pounds in own 154-day weight and 0.6 points in own score for conformation as a gilt. Selection for the index which combined productivity and growth rate was only one-sixth as great among tried boars as among boar pigs, but was five-sixths as great among tried sows as among gilt pigs. The average selection differential of parents for this index could have been greater if older boars had not been used, and if older sows had represented somewhat less than 40 percent of all females producing litters.
5. If boar and gilt pigs had been selected at random (i.e. if the numbers taken from each litter had been proportional to numbers available at weaning age), the selection for larger litters automatically would have been nearly as large as that actually obtained. The "automatic" selection was 0.62 for pigs born, 1.15 for pigs weaned, 31 pounds for weight of litter weaned, but —.21 pounds for litter average weaning weight per pig. Additional "deliberate" selection was nil for numbers farrowed, slight for numbers weaned (.25 and .09 pigs, for boars and gilts), but rather large for litter average pig weight at weaning (2.75 and 1.49 pounds, for boars and gilts). Automatic selection for litter size accounted for 27 percent of the total superiority in the indexes of the boars chosen and for 38 percent of that in the indexes of the gilts selected.
6. Opportunity for *deliberate* selection among boar and gilt pigs was utilized most fully for growth rate, less for conformation, and least for litter size. Among boar pigs, individual weaning weight received much more and conformation less emphasis than did weight at 154 days; but the reverse was true among gilt pigs.
7. Superiority of selected boar pigs in the *average* combination of sow productivity, 154-day weight and conformation score upon which actual choices appeared to have been made was found to be only 46 percent as large as if all culling had been based upon it. This corresponded to choosing boars from the best 48 percent instead of the

best 8 percent of those weaned. Superiority of gilt pigs selected was 58 percent of that expected if all culling had been based on the index apparently used, and corresponded to saving the best 61 instead of the best 33 percent of those weaned. Apparently about 50 percent of the gilts and 80 percent of the boar pigs were culled because of other factors, such as weanling weight, cryptorchids, hernias, post-weaning mortality, discrimination against pigs from younger litters and reproductive failures. Poorer utilization of opportunity for selection among boars than among gilts is attributed to excessive culling of boars by castration at weaning age, and possibly to earlier ranting of the faster growing boars, with adverse effects on conformation.

8. Linear regression of performance on time within 47 lines at five stations (364 degrees of freedom) averaged —.15, —.16 and —.22 pigs per year in litter size at birth, 21 and 56 days, respectively. Linear yearly change averaged zero for birth weight, —.19 pounds for 21-day weight, —.41 pounds for 56-day weight and —4.0 pounds (4 stations) for 154-day weight of individual pigs. Linear rise of calculated inbreeding varied from 2.3 to 3.9 percent per year.
9. Consequences of the inbreeding rise were estimated from intra-season paired comparisons of linecrosses with the parent inbred lines. Data for 325 linecrossed and 538 inbred litters representing 99 crosses of 31 lines yielded estimates of change per 10 percent of inbreeding of litter as follows: —.20*, —.35**, —.38** and —.44** pigs in litter size at birth, 21, 56 and 154 days of age; 0.02, 0.08, 0.03 and —3.44** pounds in weight per pig at these ages. Data at one station for line-crossed litters from 63 linecrossed and 50 inbred dams representing the same lines indicated the following changes per 10 percent higher inbreeding of the *dam:* —.17, —.31**, —.25*, —.28* pigs per litter at 0, 21, 56 and 154 days of age; —.06, —.11, .06 and —.13 pounds in weight per pig at these ages. Inbreeding rise for a line includes effects of inbreeding both of dam and of litter.
10. After removing expected effects of the inbreeding rise, linear change *per year* in performance of the 47 lines averaged —.03, 0.07, and —.01 for litter size at 0, 21 and 56 days of age; 0.01, —.19, —.47 and —2.8 pounds in weight per pig at 0, 21, 56 and 154 days of age. These average results indicate that selection during development of mildly inbred lines failed to improve measurably the genetic merit of the lines. At only two stations was there a positive average time-trend in total litter weight at 154 days of age after correction for inbreeding effects.
11. Linear regression of performance on inbreeding of litters, between seasons within 46 lines at four stations, indicated rates of inbreeding

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*signifies $P \leqq .05$, **indicates $P \leqq .01$ that the difference was due primarily to sampling error.

decline as large or larger than those obtained from the intra-season comparisons of linecrosses with parental inbred lines.

12. Analysis of data from 12 lines during 9 years at the Iowa station showed that line differences in rate of decline with inbreeding of litter were less than expected from sampling error for litter size and for litter weight at 154 days of age but were highly significant for pig weight at 154 days of age. There was no indication of curvilinear regression on inbreeding.
13. The apparent inability of selection within inbred lines to improve performance of crosses among the lines does not appear to be adequately explained by ordinary dominance (between none and complete) and epistasis alone, but could result from heterozygote advantage in net performance for some of the segregating chromosomal units. Small negative genetic correlations between the traits under selection would be compatible with heterozygote advantage, and could reduce the effectiveness of selection sharply, even though genetic variability remained large for individual traits. Larger positive environmental than genetic correlations also would reduce effectiveness of selection.
14. Effectiveness of selection probably was reduced because most of the selection actually practiced for litter size was automatic (i.e., would have occurred if a random sample of the pigs weaned had been chosen as breeders). Also, selection favored the less inbred pigs and dams, indicating that 8 to 12 percent of the variance in total performance was due to variation in level of inbreeding between litters within the same line and season; this reduces effectiveness of selection as much as a comparable amount of environmental variation, slows the calculated rate of inbreeding, and makes actual reduction in heterozygosity lag behind that indicated by the calculated inbreeding coefficient.
15. The foregoing results suggest that selection may be made more effective in swine if it is directed toward the improvement of crosses between complementary strains, with selection of individuals or families based upon performance of test-cross progeny.

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