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Efficiency of testing schemes in swine

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EFFICIENCY OF TESTING SCHEMES IN SWINE

by

Charles Smith

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major Subject: Animal Breeding

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INTRODUCTION

For many centuries farmers have tended to save for breeding the animals which suited their ideals, hoping thereby to improve the quality of their livestock. This method, selection for breeding of those deemed best, is still the main tool used for improving the genetic merit of farm animals.

The value of an animal is a function of what it produces and its efficiency in production. With the advance of science in agriculture, efforts have been made to find what items constitute quality of product and efficiency of production, and to develop measures which reflect differences among them reliably. Two notable examples of the latter are the Babcock test to determine the percent of butterfat in milk and the backfat probe to measure backfat thickness in live swine. Once the criteria constituting value have been established, and suitable measurements found, the process of selection and breeding can proceed.

From the animal breeding standpoint, information is required on the repeatabilities and the heritabilities of the traits and the correlations among the traits. Information of this kind has been accumulating from research in recent years and now provides a sound basis for selection and for the planning of breeding schemes.

The productive traits of farm animals are largely of a
quantitative nature. The proportion of the observed variation which is genetical depends greatly on the trait considered, but also on the conditions of production and measurement. To some extent animals can be made to develop according to some predestined order by control and manipulation of their environment. Hence measurements are relative to the conditions under which they were made, and comparisons of merit among animals may not be valid unless the animals have had an equal basis to display their merit.

The central testing station provides a basis for testing and comparing animal seedstocks under reasonably standard conditions. Presumably different designs will give different rates of improvement. How do the properties of each trait and other variables influence the choice of system? How best should the design be set up in terms of composition and numbers in the test groups? How best can the testing station results be integrated with the breeding structure of the population? What improvement can be expected from testing, and how does this compare with that possible by other means? These questions are relevant in the use of central testing stations.

The purpose of this study then, is firstly to identify more clearly than has been done heretofore, those factors which have important effects upon the genetic improvement that can be made with testing station schemes, and secondly to specify
optimum combinations of these factors which permit reasonably near maximum genetic improvement in view of the biological and practical limitations.
REVIEW OF LITERATURE

The subject matter of interest in this study is largely concerned with the theoretical and practical work done on selection and on testing systems. Furthermore, those factors which may affect improvement and alter the choice and effectiveness of various plans of testing and selection, are briefly studied.

Selection and Testing Systems

Theory in selection

Smith (1937), working under Fisher, derived a formula to express the expected genetic improvement following truncation selection in a normally distributed population. A more elaborate statistical presentation of this and other properties of the population following selection was given by Perotti (1943) and by Cochran (1951). The former also considered the effects of non-normality of the population on these properties.

Hazel and Lush (1943) showed that selection on a total score or index was more efficient than either of the methods of tandem selection or independent culling levels. In such an index the traits are weighted according to their economic values, their heritabilities and the phenotypic and genetic relationships between them. Smith (1937) presented a tech-
nique for deriving such an index, or discriminant function, and demonstrated its use in plant selection. Hazel (1943) adapted the selection index for use in animals, and devised a method for estimating genetic correlations between traits, a parameter required in the construction of the selection index. Hazel et al. (1943) showed how genetic correlations could be obtained from an analysis of covariance in a hierarchical system as the ratio of the sire component of covariance to the geometric mean of the sire components of variance. Fisher (1936) considered the use of a discriminant function to maximize apparent genetic differences between individuals.

Lush (1935) compared the relative efficiency of the progeny test and individual selection in genetic improvement. He found that under the simplest conditions there must be at least five progeny tested before the progeny test can be a more accurate indicator of the parent's breeding value than the parent's own performance. The relative value of family merit and individual merit as bases of selection was studied by Lush (1947). He showed that mass selection was more effective than family selection except when the phenotypic correlation (t) between relatives was low, and the genetic relationship (r) was high. In cases where t is greater than r, family average should play a negative role when
combined with individual performance in an index.

The statistical theory of two-stage selection was given by Cochran (1951). Earlier, working with Cochran, Dickerson and Hazel (1944a) had developed formulae to estimate the genetic gain from two-stage selection, where the first selection was based on either individual performance or pedigree information, and the second on progeny performance of the selected animals. In most cases intense culling on progeny performance was necessary else the annual genetic gain was less than could be realized by mass selection alone.

**Theoretical applications**

The approach generally used in evaluating different methods of selection and in comparing testing schemes, has been to develop the relevant formulae and estimate the genetic gain achieved for particular values of the variables featuring in the formulae. These values may be hypothetical or taken from the literature. A graphing of the gains obtained for different combinations is often given with an attempt at generalization. The following section contains studies of this sort. How closely they represent the true evaluation of different systems and the improvement expected depends upon the validity of the basic theory, upon how well the variables represent the actual situation being considered,
and upon other factors which will influence genetic gains. In few cases has actual experimental proof of the theoretical findings been attempted.

Dickerson and Hazel (1944b) compared the effectiveness of different methods of selection for growth rate of pigs and productivity of sows. Using statistics from the Iowa and Nebraska stations' swine herds, they found that at weaning time eight times as many boars and three times as many gilts as were required for breeding should be retained until 180-day weight was available, in order to maintain maximum improvement for growth rate. For sow productivity, culling two thirds of the gilts after their first litter was almost equivalent to culling three fourths of the sows after their second litter.

In a paper already mentioned, Dickerson and Hazel (1944a) examined the effectiveness of selection on the progeny test as a supplement to earlier culling. In a 20-sow herd, selecting for 180-day weight at heritabilities of .30 and .125, the annual genetic gain was reduced by retaining progeny tested sires that had been selected earlier on individual performances. For carcass traits with heritabilities of .5, later selection on progeny performance also depressed the annual genetic gains if initial selections were made on the basis of sib records. Where heritability was .1, supplementary se-
lection on progeny performance for carcass traits was only a little more effective than selection on sib performance alone. In both these examples, for 180-day weight and carcass traits, further use of one fourth of progeny-tested females did give small genetic gains. With these and other examples in different species they came to the conclusion that a regular plan of progeny testing is unlikely to increase progress and may even reduce progress unless the progeny test extends the generation interval only a little, unless the reproductive rate is low, and unless the basis for making early selections is relatively inaccurate.

Dempster and Lerner (1947) studied the optimum structure of a breeding flock of poultry, based on data from a production bred flock at the University of California. For various age distributions of the breeding flock, greater efficiency in improvement was obtained with the wide-spread use of younger birds. The optimum plan existed when 80% of the males were cockerels and 90% of the females were pullets, and when selection was based on full-sib family averages, and also on individual performance in the case of the females.

Rendel and Robertson (1950) estimated that the genetic gain in milk production in a closed herd of 100 cows under optimum conditions could be about 1% per year. One quarter of the gain comes from the early culling of heifers and the
rest comes from the selection of bulls from high producing dams. Considering the use of progeny testing with artificial insemination in dairy cattle, Robertson and Rendel (1950) estimated a maximum genetic gain of 1.5% of average yield in a unit of 2000 cows. The breeding of young males from selected proven bulls contributed 43% of the gain, while the selection of cows to breed bulls contributed 33%. Increase in the size of population increased the improvement per year. Although the heritability affected the gain per year considerably, the optimum structure of the population was relatively unchanged for values of heritability from .1 to .5. Where the number of males required in the population is low, as is made possible by artificial insemination, the accuracy of evaluation of the sire and the high selection differentials possible more than compensate for the increase in generation length through progeny testing.

Fredeen (1954) examined the effect of size and sex composition of the litter test group on the rate of genetic improvement in a closed 20-sow herd of swine. For traits directly measurable on the breeding animal selection on individual performance alone was advocated unless the heritability was very low. But for carcass traits not measurable directly on the breeding animal, indirect selection based on a litter test group comprising three males gave maximum im-
provement. Osterhoff (1956) showed that for a fixed number of progeny per test group, a more accurate estimate of a sire's breeding value is obtained by testing pigs from several litters, rather than by the conventional test group of four littermates.

The use of sire and dam family averages in increasing the efficiency of selection has been studied in general, and in poultry in particular, by Osborne (1957). He developed formulae, general for values of heritability and group size, to compare the efficiency of these different methods of selection. For low values of heritability, sire family selection is more efficient than dam family selection which in turn is more efficient than mass selection. As heritability increases, the differences in the methods are reduced, until at high heritabilities the positions are reversed. The change in the relative weight of the regression coefficients in an index combining individual, dam family and sire family performances with changes in heritability, point out where stress should be laid in selection.

If the selection to be practiced and the facilities available in a testing scheme can be specified, Robertson (1957) gave a method for estimating the optimum test group size. He was able to express the expected genetic gain in terms of the proportion selected (p) and the testing ratio (K) where K is the ratio of the number tested to the number of groups se-
lected.

\[
\triangle G = \frac{2}{p} \sqrt{\frac{a}{p+\frac{a}{K}}} \sigma_g \text{ where } a = \frac{4 - h^2}{h^2}
\]

By maximizing this expression with respect to \( p \) he was able to equate \( K/a \) to a function of \( p \), easily calculated from tables of the normal distribution. Thus one can determine, in terms of \( K/a \), the optimum value of \( p \), and hence the optimum group size, which permits maximum genetic improvement. He showed that for the optimum running of any such scheme, the intensity of selection must be at least one in four. Tolerable limits of group size, giving genetic improvement within 10% of the maximum, were quite large and increased as \( K \) increased. He concluded that the optimum plan for selection and the probable genetic superiority of chosen groups depend only on \( K \), on heritability, and on the genetic relationships within the groups.

Wearden (1957) outlined a method of determining sample size adequate to show significant differences between test groups in an analysis of variance. By specifying the probability of error and the power of the test, an iterative solution to find the adequate group size is possible from the equation

\[
n = \frac{1}{\Theta} \left[ \frac{F_B}{F_\alpha} - 1 \right]
\]
Here $\Theta = \frac{\sigma^2}{\sigma^2_w}$, and $F_B$ and $F_\alpha$ are the $F$ values corresponding to the power and to the Type I error, respectively. Robertson and Rendel (1950) state that statistical significance does not enter the problem of testing, which is essentially that of making the best use of the animals available to achieve the maximum genetic improvement per year.

**Progress from selection**

While the theoretical expectations of genetic gain from selection can be specified, what evidence exists that these expectations are fulfilled? The results of selection experiments on farm animals provide some information on this question.

Krider *et al.* (1946) reported on the first four generations of selection for rapid and slow growth rate in Hampshire swine at Illinois. The two lines had been kept as closed herds, using five boars in each line, and saving only one boar from each litter and mating each boar to the gilts least related to him. A selection differential of 181 pounds had been applied over the four generations and a difference of 23 pounds in 180-day weight realized between the lines. It has been suggested by Dickerson (1951) and Craft (1953) that the difference between the lines might have been due mostly to decreased growth rate in the slow line. The large seasonal differences in 180-day weight obscure this point. A later
report of the same experiment by Craig et al. (1956) involving ten generations, showed that selection continued to be effective in further separating the lines. The cumulative effect of selection was now 40-50 pounds. The estimates of heritability of 180-day weight in the slow growth line were less than those in the rapid line, although selection seemed to be more effective in the former. The average 180-day weight for the rapid growth line over the ten years was only 145 pounds. The inbreeding coefficient had reached 13%. The need for a control population as a base to compare the improvement in the two directions was stressed.

An experiment at Alabama to determine the effectiveness of selection for efficiency of gain was reported by Dickerson and Grimes (1947). Two lines of Duroc swine, one selected for high and the other for low efficiency of gain, were developed by selection on the basis of individual feed efficiency. The boar and gilt making the most efficient gain in each of the eight litters of the efficient line, irrespective of the level of litter performance, were selected as parents of the next generation, and similarly for the inefficient line. The intra litter selection differential over five years was 102 pounds feed per 100 pounds gain, and a difference of 25 pounds feed per 100 pounds gain was obtained between the lines. Again the seasonal variation obscured any regular trend in
improvement, but the separation of the lines was effected by selection.

Selection within mildly inbred lines of swine received major emphasis in the cooperative research of the Regional Swine Breeding Laboratory since 1937. A review evaluating the amount and the effect of this selection in inbred lines was given by Dickerson (1954) incorporating data and results from the cooperating stations. They found that the amount of selection for litter size, growth rate and conformation could have been greater than was actually practiced. After removing the expected effects of inbreeding, the average annual change in performance of 47 inbred lines was -.03 pigs for litter size at birth and -2.8 pounds in weight per pig at 154 days of age. These and other results indicated that selection had failed to improve measurably the genetic merit of the lines. There was no evidence that selection within inbred lines improved the performance of crosses among the lines. Bradford et al. (1958) also found that selection was ineffective in improving inbred lines of swine at Wisconsin. Boulware (1954) found the same for growth rate and sow productivity in a mildly inbred herd of swine originating as crossbreds. In most studies of litter size, automatic selection accounted for a greater portion of the total selection than did deliberate selection. Much of the work on selection in swine has been confounded with inbreeding programs
and consequently may not reflect fully the potential of selection.

Damon and Winters (1955) on the Chester White and Duroc herds of the Hormel Foundation found that selection was effective in bringing about small increases in the number of pigs farrowed (.076 pigs) and in average weaning weight (.191 pounds). These figures were obtained after deducting an estimate of change due to management and environment.

Rendel and Robertson (1950) estimated the genetic gains directly from the selection applied. In a dairy herd where records were analyzed, the probable improvement achieved by selection was .7% per year in milk production, although the actual value may vary between wide limits. They pointed out some of the fallacies which may exist in indirect measurement of improvement by selection such as removing trends and using age correction factors.

Selection experiments for large and small body size in mice have been described by McArthur (1949) and Falconer (1952). In both experiments selection was effective in separating the lines and response was greater in the small line. Falconer obtained a difference of 50% of the initial weight between the lines after eleven generations of selection.

Falconer and King (1953) studied selection limits in the
mouse in a cross of two strains independently selected for large body size. Both strains had reached limits of body size and no further improvement from selection was obtained. Three possible causes of the selection limit were studied viz., the loss of genetic variance incurred in selection or by inbreeding, opposing natural selection, physiological limits. Selection for large and small body size in the cross between the strains was effective, although the response was more rapid from downward selection. The authors concluded that the limitation in response of the parent strains was due to loss of genetic variance.

The generation interval is shorter and the effects of selection over many generations can be more quickly investigated in poultry than in larger farm animals. Lerner and Hazel (1947) found an increase of 5.6 eggs per year over 12 years in a flock of 400-700 pullets. Selection on family or progeny performance was emphasized, and breeding was from females two years or older. On the other hand, Lerner and Dempster (1951) and Lerner (1951) found an attenuation of genetic progress under continued selection for shank length and for egg size respectively. Lerner postulated that natural selection for optimum fitness was reducing the gains from artificial selection for other traits, a phenomenon he calls genetic homeostasis.
These experiments indicate that the gains from selection are variable and uncertain. Even with appreciable heritabilities and good selection programs, the results have often been disappointing.

**Systems of testing**

Culbertson et al. (1931) reported on a test of litter groups of four pigs submitted by pedigree swine breeders in Iowa. Performance was measured on daily gain, efficiency of gain and meat production. The test was discontinued soon after.

The pioneer work in swine testing was done in Denmark where the system developed in 1907 is still in operation with only minor alterations. The system has been described by Lush (1936), Clausen (1952), Jonsson (1957) and others. Briefly, the scheme is based on three central testing stations and 250 state approved breeding centers, with supplementary testing and breeding units. Specifications as to the numbers tested and the level of excellence are made both to the breeding centers and for entry into the herd book. A group of four litter-mates, two barrows and two gilts, is tested for rate and efficiency of gain from 20 to 90 kilograms. All four pigs are slaughtered and comprehensive carcass measurements are taken. In 1950, individual feeding replaced the hitherto group feeding practice, in the hope of getting more accurate
information (Jonsson, 1957).

The test unit of four litter-mates for the above traits at a central testing station is also used in Sweden (Johansson and Korkman, 1950), Germany (Osterhoff, 1956), Canada (Fredeen 1953) and also France, Austria, Netherlands, Poland, Finland, Norway, Portugal and Britain (United Nations, 1957). However, the results of the tests are only complementary and not so fundamental to the breeding structure of the swine industry in these countries as they are in Denmark.

In the United States central testing systems are a recent development. In general, more stress is given to individual performance through the testing and sale of boars. Munson (1957) and Sutherland (1958) have described the Iowa testing program which is based on a sire group of three boars and one barrow from at least three litters. The backfat probe of Hazel and Kline (1952) is used as an indicator of carcass merit for the boars. A review of the swine testing stations throughout the United States is given by Omtvedt (1958). Performance testing schemes have also been reported for beef cattle by Paterson et al. (1955) and Lindholm and Stonaker (1957), and for sheep by Shelton et al. (1954).

In Britain, the National Pig Breeders Association supports a scheme of litter recording on the farm, considering number and weight at birth and weaning as measures of sow
productivity and as a basis for selection among sows (Ol-
brycht, 1943).

Bernard et al. (1954) describe a system used in Wiscon-
sin to aid the breeder in selecting breeding stock on the
farm. Records on litter size at birth and 154 days, and on
weight at 56 and 154 days are sent to the University where
indexes are computed for the pigs. The breeder is sent a
list of the highest indexing gilts as an aid in helping him
select breeding stock on the basis of these indexes. Karam
et al. (1953) have derived indexes for selecting lambs under
farm flock conditions for a similar on-the-farm selection sys-
tem.

For milk production, the selection of bulls must be
based on the performance of their female relatives. In Den-
mark in 1955, there were 32 stations testing 93 sire progeny
groups (Hofmeyr 1956). The progeny group consists of 15 to
20 randomly chosen daughters which comply to certain specifi-
cations on age, health and appearance. The repeatability of
the station test on eight daughters was .70, and the corre-
sponding repeatability from station to field test was .45.
Mason (1952) and Robertson and Mason (1956) have critically
reviewed certain aspects of the test, especially with re-
gard to the low repeatability from station test to field test
and commented favorably on the large numbers possible in the
field test.

Because artificial insemination can spread a sire's progeny over many herds and because of the low heritability of herd differences ($h^2 < .1$), McArthur (1954) suggested that sires be judged by comparing their daughters with their contemporaries in the same herd. This system is being used by the Milk Marketing Board in Britain to evaluate its A.I. bulls. A discussion of the system including certain modifications, such as weighting according to the number of herds in which a bull has daughters, was given by Robertson et al. (1956). Gaunt and Legates (1955), in D.H.I.A. data in the United States, suggested that the daughter-contemporary differences had much usefulness as a corrector of some of the environmental circumstances, particularly when large differences exist between herds.

In poultry the random sample test is now widely used. A random sample of hatching eggs, intended for commercial production, is hatched and reared under identical conditions with other stocks and compared with them in productive ability. King (1952) emphasized that the random sample test provides an unbiased means of evaluating stocks in comparison with other stocks. He found a repeatability of .45 for hen-housed production of strains over three years, but quotes California tests as having lower repeatabilities. Hill and Nordskog (1956), in an experiment with ten varieties of in-
bred hybrids over three years and four locations, found a
repeatability of hen-day production of .44 at one location in
one year, but one of only .12 at different locations in dif-
ferent years. The variation of strains in different tests
can be decreased by increasing the size of the test group, un-
less there are interactions with season, year or location, in
which event testing should be done over several seasons and
locations.

Testing schemes in poultry have been designed to com-
pare breeders' stocks and their produce, rather than to give
the breeder a basis for selection within his own flock.

The results of testing

In very few cases has any attempt been made to measure
the actual amount of selection practiced on the basis of test
results. Lush (1936) compared the mean of boars whose sons
were used for breeding with the average of all boars tested
in the same years (1929-1931) in Denmark. The former showed
superiority in the desired direction in all six traits studied
indicating that fairly strong selection was being practiced
on the basis of the test results.

Lush (1936) and Clausen (1952) have shown marked changes
in the characteristics of the Danish Landrace since testing
work began. Most traits have shown marked changes at certain
times but have continued practically without change during other periods. Clausen (1952) reports increases of 4.3 cm. in length and 0.34 cm. in belly thickness, and decreases of 0.78 cm. in backfat and 0.27 feed units/unit gain in pigs tested at the stations from 1929 to 1951. Although there are many indications to support the great role of selection in these changes, Lush (1936) points out that the data need not preclude belief that steady environmental improvement may have had much importance.

Johansson and Korkman (1950) found similar trends in improvement in the Swedish Landrace. Thus from 1929-1943, daily gain had increased by about 14 grams, length, by 1.4 cm., and backfat had decreased by 0.4 cm.

Fredeen (1953), despite high heritabilities and favorable genetic correlations in his data, found no material change had occurred in any of the economically important traits of the Canadian Yorkshire during 20 years of progeny testing. He had to conclude that consistent selection on test performance had not been practiced and pointed out that there was little economic incentive to improve carcass quality.

On the other hand, Sutherland (1958) reported a substantial decrease in backfat probe of boars being tested at Iowa of 0.21 inches in one year and a corresponding 1.8% increase
in percentage lean cuts. These trends have continued into the following seasons whilst rate and efficiency of gain have shown more seasonal variation and no consistent improvement.

Non-Genetic Factors Affecting Test Performance

King (1957) states that the use of a central testing station is justified if the pre-test environment produces unimportant lasting effects on traits measured at the station, if conditions at the station are effectively constant for all pigs, and if genotype-environment interactions are unimportant.

Pre-test environment

In an inbreeding experiment on Poland China swine at Iowa, Whatley (1942) found intra-litter correlations of 180-day weight with birth weight and weaning weight of .43 and .55 respectively. On 1394 pigs the effect of age of dam was not significant although the pigs from older dams were slightly heavier at 180-days. Comstock et al. (1942) in Poland China and Minnesota No. I pigs, found intra-litter correlations between weaning weight and subsequent rate of gain, ranging from -.09 to .37. Johansson and Korkman (1950) obtained correlations of .02 and .13 between and within groups respectively for weight at three weeks with daily gain on
test. Osterhoff (1956) working on later data from the Swedish testing stations, found correlations of .24 and .21 between daily gain on test and three-week and seven-week weight respectively within the test groups, but .10 and .14 over all groupings. With respect to characters other than daily gain, the effects of pre-test environment seem not to have been studied. From the above results, it would seem that selection of heavy weaners for testing would enhance the growth rate of the test group.

**Test group selection**

Johansson and Korkman (1950) studied the representativeness of the test group in the Swedish testing program. They found a slight excess of females in spite of a normal sex ratio in the population of 51.4% males. The pigs selected for testing weighed 6.4% more at three weeks than did the average of the litter from which they were selected. There was also less variation within the test group than in the whole litter. Selection for the test resulted in a more uniform and heavier test group than if a random selection had been made. Selection was more intense in the large litters. Osterhoff (1956) obtained very similar findings in Swedish data collected in 1951 and 1952.

Limitations in selection may be imposed by regulations
on entry dates, entry weight, nipple and conformation requirements, numbers farrowed and weaned and other prerequisites.

**Genotype x environment interactions**

The general problem of heredity x environment interactions has been discussed by Haldane (1946) and with special reference to animal breeding by Hammond (1947). The latter is in favor of selecting in conditions optimum for the expression of the traits being considered. Falconer (1952) suggests that performance of one trait in two environments may be regarded as two distinct characters with a genetic correlation between them. From the size of this correlation and the heritability of the trait under the different environments, it is possible to predict the genetic gain achieved for one environment by selecting in the other. In a selection experiment for size in mice, those lines selected for size on a low plane of nutrition also did well on a high plane, whilst those selected on the high plane were unimproved on the low plane (Falconer and Latyaszewski, 1952). A selection experiment on different planes of nutrition in swine is reported by Brugman (1950), but results relevant to the above discussion are not yet available.

Jonsson (1957) reports an experiment by Clausen testing two breeding groups, Danish Landrace and native black-spotted
pigs, each on two levels of feeding. With 32 litters, and eight pigs per litter divided over the levels, there was no evidence of any interaction of breed and feeding level. Kristjansson (1957) compared pen versus pasture feeding in evaluating Canadian Yorkshire sires. Taking four litters from each of four sires, he put two pigs from each litter on the different feeding systems, and compared the ranking of the sires on different treatments for several characters. Only for loin eye area did he find a significant change of rank, but the rankings were not consistent for any trait.

Sutherland (1958) found a significant breed x season interaction for efficiency of gain in the Iowa test data, but not for rate of gain or backfat probe.

In D.H.I.A. data on daughters bred by artificial breeding, Legates et al. (1956) found no evidence of a sire x herd interaction for milk or fat production. Mason and Robertson (1956) obtained no sire x herd interaction in milk records of 13,000 cows bred by artificial insemination in Denmark. The ranking of bulls for breeding value was similar in all herds at all levels of production.

Urick et al. (1957) studied gains in Hereford steer calves at Montana over three periods -- winter feed-lot, summer pasture and second winter feed-lot. The correlation
between gains in the winter periods was .32, while the correlations of summer gain with each of the winter gains were .07 and .02. The genetic correlations were extremely high and unreasonable. Hill and Nordskog (1956) found location-year and a year-variety interactions for egg production in performance testing of ten varieties of inbred poultry hybrids at four locations over three years. They suggested that replication over years would be more effective in comparing varieties than a corresponding replication of locations.

If commercial stock are predominantly crossbred, will improvement in the purebred parent stock be transmitted to the crossbred progeny? Henderson (1949), in data representing single crosses of 12 inbred lines of Poland Chinas, found that specific combining ability accounted for a greater part of the variation in litter traits than either maternal effects or general combining ability. Bradford et al. (1958), studying inbred lines, two and three line crosses and top-crosses in swine, found that maternal effects were more important than general combining ability in weaning weights, and vice versa for five-month weight. Specific combining ability was not an important source of variation in individual pig weight. Eaton et al. (1950) reported line differences in general combining ability and maternal effects for individual weights both at 15 and 45 days in crosses among nine
inbred lines of mice, but not for litter size or total litter weight. Specific combining ability was appreciable, though not significantly larger, for viability and total litter weight, but not for individual mouse weight.

**Measurements**

Certain measurements and measurements over certain periods will be more effective than others in evaluating the worth of an animal. For example, Baker *et al.* (1943), Nordskog *et al.* (1944) and Blunn *et al.* (1955) all showed that heritability of gain in swine increases after weaning to a maximum around 112 days of age. They concluded that a measure of growth rate after weaning to over 112 days will measure the genetic growth rate most efficiently. However, Johansson and Korkman (1950), on the basis of Swedish testing data, disagreed. In their data, age at slaughter and rate of gain on test had heritabilities of .57 and .26 respectively. They concluded that daily gain from birth to slaughter is a better measure of inherent growth rate than is daily gain during the testing period.

Jonsson (1957) has discussed the advantages accruing from individual feeding of swine in testing, both in obtaining individual feed efficiency records and finding more uniformity in the growth rate of litter mates. Thus the overall standard deviation of rate of gain under group feeding was
57.1 grams and the coefficient of variation 8.3%, compared with 32.1 grams and 4.8% for individual feeding. The correlation between litter mates for rate of gain was .11 under group feeding and .36 under individual feeding. These comparisons were made using the results from group feeding in years 1948-1949, and these years showed a considerably lower correlation between litter mates than the .24 found by Lush (1936). Bean (1946) failed to find any advantage in taking three-day weights rather than a single weight at the beginning and the end of a feeding experiment with swine. Lasley and Kline (1957) and others, have examined the splitting and cutting errors in swine carcass evaluation, and have recommended suitable measures of various carcass traits.

**Year, season, sex, station and nutrition**

Many authors have shown important effects of year, season, station and sex on the performance of swine Lush (1936), Whatley (1942), Johansson and Korkman (1950) and Sutherland (1958). Fortunately, in testing work, comparisons can be made directly within each above grouping, or in different groups by comparing deviations from their group means. Such comparisons will be valid unless there are interactions which affect performance. The importance of the latter have not been established.

By controlling the plane of nutrition, McMeekan (1940)
was able to make pigs grow along predetermined growth curves and showed that carcass proportions and composition were greatly affected by differences in growth rate. Winters et al. (1949) conducted a similar experiment and showed that pigs fed at a low plane of nutrition from weaning to slaughter were more efficient in their feed conversion and were leaner. In many studies, for example Dickerson (1947), Jonsson (1957) and Sutherland (1958), rate of gain has been positively correlated with backfat thickness. Thus genotypes which yield lean carcasses on restricted diets may be excessively fat if fed ad lib. The policy of feeding adopted should depend on the aims of the improvement program.

It is possible to examine the theoretical implications of testing schemes and on this basis recommend suitable programs which should maximize genetic improvements with the testing resources available. This provides a climate in which selection, and other forces, if they are effective, can be used to the best advantage.

The actual improvement obtained following selection from various experiments and testing schemes, has sometimes been close to that expected and sometimes far below it. Skeptics may maintain that the former cases were due to favorable environmental change and the latter represent the true
potential of selection, while others may argue conversely.

There is evidence that many factors may greatly affect improvement following selection; in theoretical cases these factors may be neglected, but in practice they can be of paramount importance. Thus, from theoretical considerations alone, it will not be possible to specify exactly the best methods of improvement nor to predict the improvement expected under practical conditions. Instead, the purpose of theoretical studies is to provide a basis for action and an appreciation of some of the considerations involved in selection experiments and testing schemes.
THE INVESTIGATION
Theoretical Derivations

The object of swine testing is to give a valid basis for selection of breeding stock. These animals selected for breeding will tend to come from families whose test groups perform well for the traits considered important. One would like to estimate the genetic improvement achieved by such testing and selection, and to be able to specify those conditions which will maximize this improvement. It is possible, by making several assumptions and simplifications, to obtain a solution to this problem. The findings which follow are strictly valid only in those idealized conditions, but are likely to represent practical conditions fairly well if selection is at all effective. How well the findings actually do hold in practical conditions will depend on how closely the true biological situation is represented by the assumptions and simplifications made.

Selection on some function \(P\) of phenotype in a normally distributed population, will yield a selected group whose average genetic superiority over the unselected population will be \(\Delta G\), where

\[
\Delta G = \sum_p b_{GP} \bar{\phi} (e.g. Smith 1937);
\]
Selection is assumed to be truncation selection of superior phenotypes consisting of a proportion \((p)\) of all phenotypes, and \(z\) is the ordinate at the point of truncation; \(b_{GP}\) is the linear regression of the genotype of the animals being selected on the phenotypic basis for their selection, and \(\sigma P\) is the standard deviation of the latter. The assumption is made that the effects of the genes are additive. Only with this assumption can the heritability \((h^2)\) and the regression of \(G\) on \(P\), a function of heritability, truly represent the true fraction of the phenotypic superiority which is genetic and can be won by selection. Those heritabilities found in practice represent situations with some degree of non-additive effects and to this extent the improvement obtained on selection will not be equivalent to that obtained if the gene effects were all additive.

With this formulation of \(\Delta G\), the relative improvement from selecting for different \(G\)'s, on different \(P\)'s and at different intensities \((p)\) can be investigated. The evaluation of the efficiency of various testing schemes is a special case of this problem.

In practice, certain restrictions on \(\Delta G\) can arise. If selection is not strictly by truncation \(\Delta G\) will be reduced. Non-normality may either increase or decrease \(\Delta G\).
depending on the direction of the skewness (Perotti 1943). In the thesis heredity x environment interactions, farm and maternal effects and other effects which may otherwise complicate the evaluation of an animal will be ignored, although it is appreciated that in certain practical conditions they may be of paramount importance.

The phenotypic basis for selection (P) can be of several types. Selection can be based on individual performance or on performance of relatives. Relatives can be divided into pedigree, progeny and sib groups and the latter into sire family and dam family groups. Combinations of these groups may also be used as basis for selection, each source being weighted relative to its importance. For example, in dairy cattle the basis for selection may be an index incorporating first lactation yield, the yield of m half-sisters, and that of the dam. Because of the complications introduced by an index, only simple combinations will be considered here.

The relative efficiency of different testing schemes will be proportional to the genetic improvement they provide in the conditions under which they are being compared. The problem of comparing the efficiency of different testing schemes can be dealt with in two stages. Firstly, for each scheme those conditions which produce the maximum
genetic gain, relative to the resources, can be specified and the genetic gain at this optimum evaluated. Then secondly, on the basis of the latter, different testing schemes can be compared in efficiency.

Robertson (1957) and others have stressed that the optimum running of a testing scheme must be a compromise between accuracy ($b_{GP}$) and choice ($z/p$). The more accurate the assessment of genetic merit through increasing group size, the lower will be the selection differential, and vice versa.

It will be further assumed throughout the thesis that $\Delta G$, the annual improvement from testing, will remain constant over several generations of testing. In practice $\Delta G$ may change appreciably in successive generations.

A method for determining the optimum group size in a progeny test or sib test was given by Robertson (1957). The method was not readily adapted to swine testing, and several extensions had to be made. In swine, the economic traits are measurable on both sexes and show high heritabilities, making individual selection worthwhile. For carcass traits, the sibs tested are slaughtered and are not available for selection. As the extensions to the method are based on Robertson's formulation, his method will be brief-
ly sketched.

In any testing program there will be some total resources $R$, say $R$ dollars, allowing $N$ animals to be tested. $N$ will be some simple function of $R$ depending on the cost of testing under different schemes. On the basis of the results of the test, $T$ animals will be selected for future breeding stock, where $T$ can be greater or less than $N$. Animals will be tested in groups each of size $m$, and each group representing a family of size $n$. $S$ groups and their families will be selected on the basis of the test to make up $T$. These symbols are similar to those used by Robertson, $R$, $T$, and $n$ being introduced to make the solution more general.

Robertson proceeds as follows. The improvement ($\Delta G$) from selecting sires ($S$) based on the mean of $m$ offspring ($\bar{O}$) is

$$\Delta G = \frac{2}{p} \frac{b_{GS} \bar{O} \sqrt{P_0}}{\text{Cov} \ G_S \ (O_1 + \ldots + O_m)/m}$$

$$= \frac{2}{p} \frac{\text{Cov} \ G_S \ (O_1 + \ldots + O_m)/m}{\sqrt{P_0}}$$

$$= \frac{2}{p} \frac{r_1 \ \bar{O}^2}{\sqrt{P_0} \ \sqrt{\frac{m}{1+(m-1)t}}}$$

where $r_1 = \frac{1}{2}$ is the genetic relationship between a parent
and its offspring, $\sigma_g^2$ and $\sigma^2$ are the genetic and phenotypic variances and $t$ is the intra-test group correlation. 

i.e. $\Delta G = \frac{2}{p} \frac{h}{2} \sqrt{\frac{m}{1+(m-1)t}} \sigma_U$ where $h$ is $\frac{\sigma_U}{\sigma_p}$ under the assumption stated earlier concerning additive gene effects. Let $K = N/S$. Then since $p = mS/N, m = pK$. Assuming $t = rh^2 = \frac{1}{2}h^2$ where $r \frac{1}{2} \frac{1}{4}$ is the genetic relationship among the offspring (half-sibs) in the test group, then

$$\Delta G = \frac{2}{p} \sqrt{\frac{m}{m+a}} \sigma_U \quad \text{where} \quad a = 4 - \frac{h^2}{h^2}$$

$$= \frac{2}{p} \sqrt{\frac{p}{p + a}} \frac{K}{a} \sigma_U.$$ 

Differentiating $\Delta G$ with respect to $p$ and equating to zero gives the maximum for $\Delta G$ with respect to $p$.

Thus $\frac{K}{a} = \frac{2px - z}{2p(z - px)}$.

Thus he equated $K/a$ to a function of $p$ easily calculated from the tables of the normal distribution. For any value of $K/a$ one can determine the optimum $p$ and hence the optimum group size $m$, and therefore also the maximum genetic gain. He also considered the effect of non-genetic differences be-
between groups, consisting of a proportion \( c^2 \) of the total variance; i.e., \( t = rh^2 + c^2 \). The same procedure is valid both in determining optimum group size and maximum genetic gain if \( a = \frac{4-h^2-4c^2}{h^2+4c^2} \), and the value of \( \frac{Z}{P} \sqrt{\frac{P}{P+a}} \)

found for \( K/a \) is multiplied by \( \sqrt{\frac{h^2}{h^2+4c^2}} \). Where the genetic relationship within the test group (\( r \)) is not equal to the square of the genetic relationship (\( r^2_1 \)) between the test group and the animals selected, as in the half-sib test, the factor \( \frac{Z}{P} \sqrt{\frac{P}{P+a}} \) found for \( K/a \) must be multiplied by \( \frac{r_1h}{\sqrt{t}} \).

The above cases include the progeny test proper, and sib selection where the individuals tested are not included among those selected and when the size of the test group (\( m \)) does not naturally reduce the number available for selection. An example of the latter is selection of cocks on the performance of their sisters.

To extend the method to swine testing, where the individual is relatively more important and slaughter tests are practiced, the following three cases are considered.

Selection may include:
(1) only tested animals, 
(2) tested animals and their relatives, and 
(3) only relatives of tested animals. 

The first two cases include selection of the individual, and the third represents the slaughter test. 

In case (1) where only tested animals are used to provide the future breeding stock, the genetic superiority following selection is 

\[ \Delta G = \frac{z}{p} \cdot b_{GP} \sigma_P \]  
where \( p = \frac{T}{N} \). 

Where the animals are tested in groups of \( m \), with \( r \) and \( t \) the respective genetic and phenotypic correlations within the groups, 

\[ \Delta G = \frac{z}{p} \cdot \frac{\text{Cov} \left[ \frac{(G_1 + \ldots + G_m)}{m} \right] \left[ \frac{(P_1 + \ldots + P_m)}{m} \right]}{\sigma_P} \]

\[ = \frac{z}{p} \cdot \frac{1+(m-1)r}{m} \cdot \frac{m}{\sqrt{1+(m-1)t}} \cdot h \sigma_G \]  

The intensity of selection \( (p) \) will be the same for both
individual and group selection since \( p = \frac{mT}{mN} \). It only re-
mains to evaluate \( J = \frac{1 + (m-1)r}{m} \frac{m}{1 + (m-1)t} \) for values of \( r, t \) and \( m \). The maximum value for \( J \), for given values of \( r \) and \( t \), represents the optimum group size \( (m) \) and gives the maximum genetic improvement.

In case (2) both the tested animals and their relatives are available for selection. The average genetic superiority following selection is

\[
\Delta G = \frac{Z}{p} \frac{\text{Cov} \left[ \frac{G_1 + \ldots + G_n}{n} \right] \left[ \frac{P_1 + \ldots + P_m}{m} \right]}{\sigma^2_p}
\]

\[
= \frac{Z}{p} h \sqrt{\frac{1 + (n-1)r}{n} \frac{m}{\sqrt{1 + (m-1)t}}}
\]

The family size \( (n) \) will be constant for any particular case and \( r \) will be known. Thus \( \Delta G = \frac{Z}{p} Q \sqrt{\frac{m}{1 + (m-1)t}} \) where

\[ Q = h \sqrt{\frac{1 + (n-1)r}{n}} \]

is unaltered by changes in \( m \). If \( T \) animals are required \( S = T/n \) and \( K = N/S = nN/T \). \( p = mT/nN = m/K \), so \( m = pK \) as before.

Hence \( \Delta G = \frac{Z}{p} Q \frac{1}{\sqrt{p + \frac{a}{K}}} \).

Then \( K/a \) can be expressed again as a function of \( p \), and the optimum group size \( (m) \) and maximum genetic gain \( \Delta G_{\text{max}} \) can be obtained. Since \( K = Nn/T \), \( K \) will change as family size \( (n) \) changes.

*More exactly \( \Delta G = \frac{Z}{p} h \sqrt{\left( \frac{1 + (n-1)r_2 + (n-m)r_1}{n} \right) \frac{m}{\sqrt{1 + (m-1)t}}} \), where \( r_2 \) is the genetic relationship within the test group, and \( r_1 \) the genetic relationship between the test animals and their relatives. Generally the test group composition will correspond to the family composition, i.e., \( r_1 = r_2 \).*
If the tested animals are not available for selection, as in a slaughter test (case 3), there will be \((n-m)\) animals left per family. Then \(S = \frac{T}{n-m}\).

\[
K = \frac{N}{S} = \frac{(n-m)N}{T} = (n-m)V \quad \text{where} \quad V = \frac{N}{T}
\]

\[
p = \frac{m}{(n-m)} \frac{T}{N} \quad \text{or} \quad m = p(n-m)V = \frac{pnV}{1+pV} \quad \text{and} \quad K = \frac{nV}{1+pV}.
\]

Since \(K = (n-m)V\), \(K/a\) is a function of \(m\) and hence of \(p\), and is not a constant with respect to \(p\) as before. The improvement \((\Delta G)\) from selection is

\[
\Delta G = \frac{Z}{p} \operatorname{Cov} \left[ \frac{(G_m+1 \ldots G_n)}{(n-m)} \left[ \frac{(P_1 \ldots P_m)}{m} \right] \right]
\]

\[
= \frac{Z}{p} \cdot h \sigma G \cdot \sqrt{\frac{m}{1+(m-1)t}}
\]

\[
= \frac{Z}{p} Q' \cdot \sqrt{\frac{m}{m+a}} \quad \text{where} \quad Q' = \frac{h \sigma G \cdot r}{t} \quad \text{and} \quad a = \frac{1-t}{t}
\]

\[
= \frac{Z}{p} Q' \cdot \sqrt{\frac{p}{p+a(1+pV)}}
\]

\[
\log \Delta G = \log Z - \log p + \log Q' + \frac{1}{2} \log p - \frac{1}{2} \log \frac{pV(n+a)+a}{nV}
\]

\[
\frac{d \log \Delta G}{dp} = \frac{x}{Z} - \frac{1}{p} - 0 + \frac{1}{2p} - \frac{1}{2} \frac{nV}{pV(n+a)+a} \cdot \frac{V(n+a)}{nV}
\]

\[= 0 \quad \text{at} \quad \log \Delta G \quad \text{a maximum with respect to} \quad p.\]

Since \(\Delta G\) is a maximum when \(\log \Delta G\) is a maximum, \(\Delta G\) is a maximum when
\[ \frac{x}{z} \cdot \frac{1}{2p} = \frac{1}{2} \left( \frac{1}{p} + \frac{1}{a} \right) V(n+a) \], i.e.,

\[ \frac{V(n+a)}{a} = \frac{2px - z}{2p(z-px)} \]

The right hand side of this equation is the same function of \( p \) as was already found. Hence using values of \( \frac{V(n+a)}{a} \) one can determine the optimum \( p \) and in turn, the optimum group size and maximum genetic gain as before.

The development of the above formulae to cover the three cases of selection specified, extends the use of Robertson's method to swine testing. By introducing \( T \) and \( n \) the method becomes more general allowing, for example, its use in the problems connected with breeding structure and population improvement studied later in the thesis.

In a testing program recommendations as to the best method of selection, the composition and size of the test group would be useful. On the basis of the above work such recommendations can be made. The procedure is to determine first the optimum size and composition of the test group for each method, and then to compare the methods at their respective optima.

If only tested animals are selected (case 1), \( p = T/N \) and the maximum genetic gain will be when \( J = \frac{1+(m-1)t}{m} \sqrt{\frac{m}{1+(m-1)t}} \)
is a maximum. Values of $J$ for $r = .5$ and .25, $t = .05$ to .5 and $m = 2$ to 100 can be quickly calculated from Table 1. Where both tested animals and their relatives are selected (case 2), given the value of $K/a$, the optimum value of $p$ can be found either from Table 2 or from the graph of $p$ and $K/a$ given by Robertson. Since $m = pK$ the optimum size ($m$) of the test group can be determined and hence the maximum genetic gain may be evaluated. The solution is similar for case 3, where only the relatives of the test animals are selected, except that $\frac{V(n+a)}{a}$ replaces $K/a$, and $m$ equals $\frac{pnV}{(1+pV)}$ instead of $pK$.

The values of $p$, $x$ and $z$ are approximations from the tables of the normal curve. Hence $\frac{2px - z}{2p(z-px)}$, equal to $K/a$ or $\frac{V(n+a)}{a}$, may not be precise especially if $p$ is small. The $K/a$ and $\frac{V(n+a)}{a}$ values given by the data will yield approximate values of $p$, and hence of $z/p$. The optimum group size ($m = pK$) will be taken as the nearest whole number, in turn changing $p$. These approximations are not serious and introduce no consistent bias. They do, however, tend to make rigorous checking of the calculations quite difficult.

A Practical Application

The methods developed above, will be demonstrated in an example selected to include a wide variety of swine testing
Table 1. Values of $1+(n-1)t$, their inverses and their square roots for common values of $n$ and $k$

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Table 2. Values of $z/p$, $K/a$ and $(z/p)\sqrt{\frac{p}{p + a/K}}$ for values of $p$

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schemes. In this example, the ratio of the number tested (N) to the number required for future breeding stock (T) is given values from 100 to .01. The family group (n) may consist of four or ten full-sibs (r = .50) or of 40 or 100 half-sibs (r = .25). The phenotypic correlation within groups (t) is considered for values from .05 to .5. The heritability of the character being selected is unspecified although of course, t = rh^2 + c^2.

The calculations

When only tested animals are used to supply the future breeding stock (case 1), p = T/N. Since p is less than unity, T cannot be greater than N. When N is greater than T the optimum test group size (m) is that which maximises J (page 40) for given values of r and t. The group size (m)
is not variable at will but is limited by the biological nature of the species as to the number within the family group. Given the family size, which is the limit of m, the maximum gains can be readily obtained and are presented in Table 3. Only at high r's and low t's is group selection superior to individual selection.

The finding by Robertson that for the optimum running of a testing scheme, the intensity of selection must be at least one in four, does not hold true at low values of N/T. For the above property to hold true in such cases, the optimum group size would have to be less than one. As this is not possible the maximum gains at low values of N/T will be obtained when m = 1 and p = 0.5. For example if T is greater than N/2, the maximum genetic gain will be obtained at p = ½. The remainder of the breeding stocks required, (T - N/2), should be selected at random from the original population. Selection of test animals which are below the mean will reduce the genetic gain from that expected by choosing untested stock instead.

Considering case 2, where both the tested animals and their relatives are selected, it was shown that

\[ \Delta G = \frac{2}{p} \cdot \frac{Q}{\sqrt{t}} \cdot \frac{1}{\sqrt{p + \frac{s}{p}}} \]
Table 3. The maximum genetic gains \( G = \frac{\Delta G_{\text{max}}}{h \sigma_G} \), the optimum group size \( (m) \) and tolerable limits \( (TL) \) for group size in selecting tested animals

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<td>( TL )</td>
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<td>( m )</td>
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For values of $K/a$ the genetic improvement ($\Delta G_{\text{max}}$) can be found directly from the graph of $K/a$ and $\Delta G_{\text{max}}$ given by Robertson or from Table 2, and multiplying by the factor

$$Q = \frac{1}{\sqrt{t}} \cdot \frac{1}{\sqrt{n}} \cdot \frac{1}{\sqrt{t}} = \frac{1}{\sqrt{n}} \cdot \frac{1}{\sqrt{t}}$$

where $Q = \frac{1+(n-1)r}{n}$. For example

at $N/T = 10$, $n = 4$, $r = \frac{1}{2}$, $t = .3$ and $a = 2.33$

$$K/a = N/T \times n/a = 17.2;$$

Then $\Delta G_{\text{max}} = .63 \times 1.83 \times 1.42 \times h \sigma_G = 1.62 h \sigma_G$

and $m = pK = 40 \times .07 = 3$ (approx.)

and similarly for other values of $N/T$, $n$, $r$ and $t$. These results are shown in Table 4.

There is no check against selecting group size ($m$) either greater than $n$ or less than one. Hence for each set of variables $m$ was evaluated as well as $\Delta G_{\text{max}}$. If $m > n$ or $m < 1$ the real improvement ($\Delta G_{\text{max}}$), putting $m = n$, or $m = 1$ was calculated. For example with the following specifications, $N/T = 100$, $n = 10$, $t = .1$ and $r = .5$, $K/a = 111$.

Thus $\Delta G_{\text{max}} = 3.44 h \sigma_G$ and $m = 20$. But $m \not> n$, so let $m = n = 10$. Then $p = .01$ and $\Delta G_{\text{max}} = 3.36 h \sigma_G$, the true maximum genetic gain.

Again at $N/T = .5$, $n = 4$, $t = .3$ and $r = .5$, and $K/a = .86$. $\Delta G_{\text{max}} = .65 h \sigma_G$ and $m = .43$. Let $m = 1$, then $p = .5$ and $\Delta G_{\text{max}} = .50 h \sigma_G$, the real maximum genetic gain.

Where only the $(n-m)$ relatives of the test group are
Table 4. The maximum genetic gains \( G = \Delta G_{\text{max}}/hC_2G \), the optimum group size \( m \) and tolerable limits (TL) for group size, in selecting tested animals and their relatives

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<tr>
<td></td>
<td>.02 1 1</td>
<td>.11 1 1</td>
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</table>
selected (case 3), given the value of $V(n+a)$ the optimum $p_a$ can be read from Table 2. Hence the optimum group size and the maximum genetic gain can be obtained. For example, where $V = N/T = 100$, $r = .25$, $t = .1$ and $n = 40$, $V(n+a) = 533$. Hence $p = .006$ and $\Delta G_{\text{max}} = 2.85 \times .25 \times 2.50 \times \sigma_G = 1.78 \times \sigma_G$.

The results for other combinations of $N$, $T$, $n$, $r$ and $t$ given in the original example are shown in Table 5. Here $m$ is never greater than $n$ since $(n-m)$ would be negative. As before, cases where $m < 1$ were corrected putting $m = 1$ and calculating the true $\Delta G_{\text{max}}$.

In these calculations Table 1, containing values of $1+(n-1)t$, their inverses and their square roots, for common values of $n$ and $t$, proved extremely useful.

The comparisons

From inspection of Tables 3, 4 and 5 comparisons can be made for a wide range of values in $N/T$, $n$, $r$ and $t$ of the maximum genetic gains obtained from various systems of testing and selection. The significance of differences in the type of family and in the size of family within each method of selection can be investigated. Finally the different methods of testing and selection can be compared, each at its optimum.
Table 5. The maximum genetic gains \((G = \Delta G_{\text{max}}/h^2_g)\), the optimum group size \((m)\) and tolerable limits \((TL)\) for group size, in selecting the relatives of tested animals

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As N/T decreases, the maximum genetic gain, ($\Delta G_{\text{max}}$) also decreases. At low values of N/T, (e.g. N/T = .01), $\Delta G_{\text{max}}$ may be very small even with the best method of selection and the testing work will be scarcely worthwhile.

The larger the family size (n), within a family type, the greater is the genetic improvement. Thus the genetic improvement from families of ten full sibs is always greater than that from those of four full sibs, and that from families of 100 half-sibs greater than that from those of 40 half-sibs. This illustrates the advantage of having as many relatives as possible to each potentially selected test group.

The optimum group size (m) falls as t increases, and if $h\sigma_G$ is constant, the genetic gain ($\Delta G_{\text{max}}$) also falls. The value of reducing environmental and any effects other than genetic, common to a family group, and hence of reducing t, is clearly shown by these tables. At low ratios of N/T m will be near or equal to one and the value of t will not be so important.

At low values of N/T the maximum genetic improvement will be when m = 1. Yet selection or rejection of a whole family of ten or 100 sibs on the basis of one record would not be realistic. At low values of N/T, some other scheme of testing would surely be invoked.
These points can be demonstrated well if a few particular cases are illustrated. In the graphs that follow the maximum genetic gain divided by $h\sigma_G$ ($\Delta G_{\text{max}}/h\sigma_G$) is plotted against $\log N/T$. Both in the preceding tables and in the graphs which follow, the genetic gains are given as $\Delta G_{\text{max}}/h\sigma_G$. The actual amount of improvement will depend to a great extent on the size of $h\sigma_G$, or $h^2\sigma_P$. However, for purposes of comparing different methods of selection on the same character, $h\sigma_G$ will be constant. Hence the comparisons hold at all levels of $h\sigma_G$, subject to the use of appropriate values of $t$. Changes in $t$ ($r h^2 + c^2$) are regarded as being due either to changes in $r$ or in $c^2$.

The genetic gains possible from full-sib families of ten and of four with $t$ values of .2 and .4 are shown in Figure 1. Selection here includes both tested animals and their relatives (case 2). In Figure 2, the genetic gains from selecting the relatives of test animals (case 3) from half-sib families of 100 and 40, for $t$ values of .05 and .2 are shown. $\Delta G_{\text{max}}$ decreases as $\log N/T$ almost linearly for the greater part of the range of $N/T$, but becomes very small when $N/T = .01$. The larger the family size ($n$) the greater is $\Delta G_{\text{max}}/h\sigma_G$, the graphs for different values of $n$, for the same $t$, being almost parallel. The effect of differences in the size of $t$ is greater when $t$ is low since changes in the
Figure 1. The maximum genetic gains \( G = \frac{\Delta G_{\text{max}}}{h \sigma_G} \) from selecting tested animals and their full-sib relatives, for the values of \( N/T \), \( n \) and \( t \) shown.

Figure 2. The maximum genetic gains \( G = \frac{\Delta G_{\text{max}}}{h \sigma_G} \) from selecting the half-sib relatives of tested animals, for the values of \( N/T \), \( n \) and \( t \) shown.
values of \( \frac{1+(m-1)t}{m} \) with changes in \( t \) are greater when \( t \) is low.

Testing can be based on sire family groups or dam family groups. In the former \( n \) will be larger but \( r \) and \( t \) will be less, where \( r \) and \( t \) are the genetic and phenotypic correlations between animals in the family. While increases in \( n \) and decreases in \( t \) cause \( \Delta G_{\text{max}}/h \sigma_G \) to increase, the decrease in \( r \) will cause \( \Delta G_{\text{max}}/h \sigma_G \) to decrease. To show the net effect of these changes in particular situations, Figures 3 and 4 have been drawn, plotting \( \Delta G_{\text{max}}/h \sigma_G \) against \( \log N/T \). The genetic gains possible from testing test groups from full-sib families of four \((r = .5, t = .3)\) with those from half-sib families of 40 \((r = .25, t = .1)\) are compared in Figure 3. Here selection includes the whole family (case 2). A similar comparison of full-sib families of ten \((r = .5, t = .1)\) and half-sib families of 100 \((r = .25, t = .05)\) where only the relatives are selected (case 3) is shown in Figure 4. In one case full-sib family selection is slightly superior at high values of \( N/T \), but this superiority is soon lost as \( N/T \) decreases when half-sib selection becomes more effective. The values ascribed to \( n \) and \( t \) can alter the crossover points appreciably, and will determine whether full-sib or half-sib testing is preferable for a given value of \( N/T \).

Selection may include only tested individuals (case 1), or both the tested individuals and their relatives (case 2),
Figure 3. Comparison of the maximum genetic gain ($G = \frac{aG_{\text{max}}}{h\sigma_G}$) obtained by selecting tested animals and their relatives for full-sib and half-sib families for the values of $N/T$, $n$ and $t$ shown.

Figure 4. Comparison of the maximum genetic gains ($G = \frac{aG_{\text{max}}}{h\sigma_G}$) obtained by selecting the relatives of tested animals for full-sibs and half-sib families, for the values of $N/T$, $n$ and $t$ shown.
or their relatives alone as in the slaughter test (case 3). The relative efficiency of those three methods of selection under the range of conditions considered can be compared by inspection of Tables 3, 4 and 5. To illustrate a few particular cases, Figures 5 and 6 were drawn, plotting $G_{\text{max}}/hG$ against $\log N/T$ as before. The relative efficiency of the three methods of selection in full-sib families of four for $t = .3$ is shown in Figure 5 and that for half-sib families of 40 for $t = .1$ in Figure 6. At high levels of $N/T$ individual selection is superior to the other two types of selection, but where $t$ is low and $n$ is small so that $n = m$, improvement from selection of individuals and their relatives (case 2) will be equivalent to selecting only tested animals. When $T = N$ the improvement from selecting tested individuals only is of course zero. The graph falls sharply just before the zero point ($\log N/T = 0$) and even at $N/T = 2$ or 5, considerable improvement is still possible by individual selection. Selection on the tested animals and their relatives (case 2) is always superior to that on relatives alone (case 3). The smaller the family size ($n$) the greater the difference will be, since proportionately fewer relatives will be available for selection after testing. As $N/T$ decreases these differences are gradually reduced.

From these particular cases presented in Tables 3, 4 and 5 and graphs 1 to 6, the relative effects and importance of
Figure 5. The maximum genetic gains from full-sib families of four from these methods of selection, viz. selection on (I) tested individuals, (II) tested individuals and their relatives (III) the relatives only, at the values of N/T, n and t shown.

Figure 6. As for Figure 5, but for half-sib families of 40.
the respective variables N/T, n, r and t can be studied. The types of testing and selection which yield maximum genetic gains depend to a large extent on the value of N/T. Complete testing and accurate evaluation is essential at high values of N/T, whereas large family size is important at low N/T. As t increases, relatively less information is gained from testing many animals per family.

The optimum system of testing and selection then is largely a function of the particulars of the situation at hand. It will depend on the character being tested for, the numbers available per family, the number required on the basis of the test, the testing facilities and so on. Thus a much more comprehensive appreciative outlook of testing schemes is achieved through the above formulations, and a basis for making recommendations and decisions with regard to testing work is available.

One of the questions which has concerned investigators in the past, the optimum test group size, can now be seen in retrospect to be a function of the conditions and not in itself an intrinsic attribute of testing. In general, the higher the accuracy required in the evaluation, the greater will be the test group size. At low values of N/T, large numbers available for selection are more important than accuracy, and test group size becomes small. If the intra-group correlation:
(t) is large, little extra information is gained by testing many animals per group, and vice-versa if t is low. As family size (n) gets larger, the accuracy required and the opportunity of increasing group size (m) tend to give a larger optimum test group size.

Some idea of the range possible in group size without appreciably decreasing the improvement is desirable. Robertson (1957) suggested tolerable limits of group size such that genetic gain would be within 10% of the maximum genetic gain. The tolerable range in group size, he found, depended more on \( K = N/S \) than on \( h^2 \).

The tolerable limits of group size were found empirically for the above problem and are shown along with the other results in Tables 3, 4 and 5. The tolerable range in group size is restricted at its one end and by the family size (n) and at its other by the minimum group size of one. All three variables \( N/T \), n and t affect the tolerable range in group size but, from these tables, it is not possible to study the effect of any one of them independently. In general it appears that the smaller the optimum group size, the smaller is the tolerable range in group size.

One deficiency of the above presentation is that individuals of mediocre performance may still be superior in merit to relatives of the best animals, yet the latter would be se-
lected. For example take two animals with phenotypes $X_1$ and $X_2$ and $X_1$ is superior to $X_2$. Selection of $X_2$ over the sib of $X_1$ will be preferable if $h^2X_2 > rh^2X_1$, i.e. $X_2 > rX_1$. On this basis the best combination of individuals, full-sibs and half-sibs in selection can be obtained. Animals at $X$, the truncation point for individual selection, will be genetically equal to those at $X/r$ in the sib population. Given $X$, one can find from the tables of the normal distribution the proportions cut off in each group. The proportions of individuals, full-sibs and half-sibs cut off by truncation at different points in the distribution of individuals are shown in Table 6. If each individual has three full-sibs and 40 half-sibs then the total number selected $T = N(p_1 + 3p_2 + 40p_3)$ where $p_1$, $p_2$ and $p_3$ are the proportions selected in the respective groups. The $N/T$ value for any value of $X$ can thus be found, as shown in Table 6.

The distributions of the different populations are shown in Figure 7, and the relative proportions of individuals, full-sibs and half-sibs comprising $T$ at different levels of selection are shown in Figure 8.

Selection of a family is more likely to be based on the mean ($\bar{X}$) of a test group, than on one individual ($X$). In this case the expected genotypic value of the test group would be $h^2 \frac{1+(m-1)t}{1+(m-1)t} \cdot \bar{X}$, of full sibs to the test group $\frac{1}{2}h^2 \frac{m}{1+(m-1)t} \bar{X}$. 
Table 6. Truncation at $\bar{X}$ in the distribution of tested animals yields proportions $p_1$ in the individual, $p_2$ in the full-sib and $p_3$ in the half-sib distribution, valuations of $N/T$ also given presuming 3 full-sibs and 40 half-sibs per individual tested.

<table>
<thead>
<tr>
<th>$X$</th>
<th>$p_1$</th>
<th>$p_2$</th>
<th>$p_3$</th>
<th>$N/T$</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.0</td>
<td>.001</td>
<td>.0</td>
<td>.0</td>
<td>750</td>
</tr>
<tr>
<td>2.5</td>
<td>.006</td>
<td>.0</td>
<td>.0</td>
<td>160</td>
</tr>
<tr>
<td>2.0</td>
<td>.023</td>
<td>.0</td>
<td>.0</td>
<td>44</td>
</tr>
<tr>
<td>1.5</td>
<td>.067</td>
<td>.001</td>
<td>.0</td>
<td>14</td>
</tr>
<tr>
<td>1.25</td>
<td>.106</td>
<td>.006</td>
<td>.0</td>
<td>8</td>
</tr>
<tr>
<td>1.00</td>
<td>.159</td>
<td>.023</td>
<td>.0</td>
<td>4</td>
</tr>
<tr>
<td>.75</td>
<td>.227</td>
<td>.067</td>
<td>.001</td>
<td>2</td>
</tr>
<tr>
<td>.50</td>
<td>.309</td>
<td>.159</td>
<td>.023</td>
<td>60</td>
</tr>
<tr>
<td>.25</td>
<td>.401</td>
<td>.309</td>
<td>.159</td>
<td>13</td>
</tr>
<tr>
<td>.10</td>
<td>.460</td>
<td>.421</td>
<td>.345</td>
<td>.06</td>
</tr>
<tr>
<td>.00</td>
<td>.500</td>
<td>.500</td>
<td>.500</td>
<td>.05</td>
</tr>
</tbody>
</table>

and of half-sibs $\frac{1}{4}h^2 \frac{m}{1+(m-1)t} \bar{X}$. Knowing $m$ and $t$, a similar solution of the optimum combination of the groups can be found.

When $N/T$ is large, it has been shown that almost all the family will be tested to achieve maximum improvement; that is $m$ will tend to $n$ if $N/T$ is large. If $N/T$ is low, the individuals superior to the sibs of the best animals would if selected form only a small percentage of total number selected, and the effect of their inclusion or omission would be small. Thus perhaps the deficiency in the methods previously used in that the sibs of the best animals will be selected in preference to mediocre test animals even though the latter may be slightly superior, will not be serious.
Figure 7. The distributions of the expected breeding value of an animal \( g_T \), that of its full-sibs \( g_{FS} \) and of its half-sibs \( g_{HS} \).

Figure 8. The percentages of individuals (IND), full-sibs (F.S.) and half-sibs (H.S.), composing T, from truncation of the curves in Figure 7 at \( X \), and assuming 3 full-sibs and 40 half-sibs per tested individual.

Figure 9. The means from initial and secondary selections in a normal population.
All animals above the mean, and all their relatives have potential for improvement. The mean of these selected in a second truncation can be found. Suppose initial selection has occurred giving $p_1$, $X_1$ and $z_1$, and further selection of the remaining group is practiced. Let the mean of the second selected group be $Y$. If no initial selection had occurred, the same truncation would give $p_2$, $X_2$ and $z_2$ as shown in Figure 9.

Now

$$\frac{p_1}{p_2} \frac{z_1}{p_1} + \frac{p_2 - p_1}{p_2} \bar{Y} = \frac{z_2}{p_2}$$

$$z_1 + (p_2 - p_1) \bar{Y} = z_2$$

or

$$\bar{Y} = \frac{z_2 - z_1}{p_2 - p_1}.$$ 

Thus the mean of the group resulting from secondary selection can be obtained.
A testing scheme cannot be regarded as a separate entity in a livestock improvement program. Its effectiveness will depend on the use made of the information from testing, considering the livestock population as a whole. To what extent selection is based on test results, how the breeding policies of the breeders are affected, how the improvement is accumulated in the breeding stock and how quickly the improvement is transmitted from tested herds to the greater bulk of the population are relevant questions in measuring the efficiency of a testing scheme.

To specify that a particular testing scheme is most suitable for a certain livestock improvement program requires, besides knowledge of the variables already studied, information on population size, population structure, methods of breeding and so on.

In general, farm livestock show a stratified structure as regards breeding operations (eg. Hagedoorn, 1948, p.217). The commercial stock are sired by pedigreed males produced in multiplier pedigree herds which in turn buy most of their sires from a select nucleus group of herds. For example, Robertson and Asker (1951) found this structure in the British Freisian, there being 20-30 elite nucleus herds.
Other breeds and species seem to follow a similar pattern. Differences in genetic merit between the breeding groups are uncertain and often small (e.g. Robertson and McArthur, 1955), but the breeding structure is well accepted.

With this breeding structure in mind, the stage at which testing is performed is seen to be important. The gains from testing and selecting solely in the multiplier pedigree herds would continually be diluted on bringing in unimproved sires from the untested nucleus group. In this case there could be little accumulation of improvement. It would seem that testing schemes should apply principally to the nucleus herds or equally to all pedigree herds if no nucleus group existed.

It is possible to study the accumulation of improvement through selection from a testing scheme and its subsequent transmission throughout the whole population, and to evaluate which system of testing and mode of transmission combine to give the maximum improvement over the whole population.

Where every pedigree breeder has the same chance of testing his stock in a testing scheme, the system will be called an open system of testing. On the other hand, if testing facilities are restricted to breeders within the nucleus group, it will be called a nucleus system of testing (Hagedoom 1948).
The open system of testing

Let $T$ be the number of animals selected on the basis of the test, and $W$ the number required for future breeding stock in the whole pedigree population, so that $T/W = q$ and $q < 1$. The accumulation of improvement in the pedigree population over the generations ($y$) is traced below in Table 7. For simplicity consider selecting only males.

Table 7. The accumulation of improvement in the pedigree herds from testing by the open system

<table>
<thead>
<tr>
<th>Generation</th>
<th>Mean of the pedigree population</th>
<th>Mean of selected males</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>$\Delta G$</td>
</tr>
<tr>
<td>1</td>
<td>$\frac{3}{2}q \Delta G$</td>
<td>$\frac{5}{2}q \Delta G + \Delta G$</td>
</tr>
<tr>
<td>2</td>
<td>$\frac{3}{2} \left[ q(\Delta G + q \Delta G) + (1-q)q \Delta G \right] = \frac{3}{2} q \Delta G$</td>
<td>$\frac{5}{2} q \Delta G + \Delta G$</td>
</tr>
<tr>
<td>3</td>
<td>$\frac{3}{2} q \Delta G$</td>
<td>$\frac{5}{2} q \Delta G + \Delta G$</td>
</tr>
<tr>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>$y$</td>
<td>$\frac{y}{2} q \Delta G$</td>
<td>--</td>
</tr>
</tbody>
</table>
At the $y^{th}$ generation the mean $G_y$ of the pedigree population is $\frac{V}{2} \Delta G q$, where $\Delta G$ is the average genetic superiority of males selected on the basis of the test, and $q$ is the proportion they comprise of all males used in pedigree herds. Similarly including the females in the selection, the mean of the pedigree population after $y$ generations $(G_y^f)$ is $\frac{V}{2}(\Delta G_m q_m + \Delta G_f q_f)$, where $m$ and $f$ refer to males and females respectively.

The next problem is to find the combination of $q$ and $\Delta G$ which will maximize $G_y$, where $\Delta G = \frac{Z}{P}$. In the notation previously used, $p = \frac{nT}{nN} = \frac{mW}{nN}$. The three variables $m$, $q$ and $p$ are interdependent and it is not possible to express $m$ and $q$ in terms of $p$ alone as before. Hence differentiation and maximization with respect to $p$ is not possible.

For any particular value of $q$, $\frac{K}{a} = \frac{Na}{Wa} \frac{1}{q}$ is known so $\Delta G_{\text{max}}$ can be found by the methods shown earlier. Hence $G_y = \frac{V}{2} \Delta G_{\text{max}} q$ can be calculated for different values of $q$, and finally the value of $q$ which maximizes $G_y$ can be found. For example let $\frac{K}{a} = 10$ at $q = 1$, then $\frac{K}{a}$ is known for other values of $q$. Given the value of $\frac{K}{a}$ the value of $\frac{Z}{P} \sqrt{\frac{P}{p+a}}$ can be easily found, as shown in Table 2. But $\frac{Z}{P} \sqrt{\frac{P}{p+a}} = \Delta G_{\text{max}} C$ where $C$ is a constant with respect to $q$. 

involving $h^2, n, r$ and $t$. If both tested animals and their relatives are selected (case 2), $1/C = h^2 \sigma_G \frac{1}{t} \cdot \frac{1+(n-1)r}{n}$ which will be constant for any given testing scheme. Hence $\Delta G_{\text{max}} \cdot q = G_y$ can be found for different values of $q$, as shown in Table 8.

Table 8. The relative genetic improvement ($G_y = \Delta G_{\text{max}} \cdot q$) for different values of $q$, if $K/a = 10$ when $q = 1$

<table>
<thead>
<tr>
<th>$q$</th>
<th>$K/a$</th>
<th>$\Delta G_{\text{max}} \cdot q$</th>
<th>$G_y = \Delta G_{\text{max}} \cdot q$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>10</td>
<td>1.24</td>
<td>1.24</td>
</tr>
<tr>
<td>.9</td>
<td>11.1</td>
<td>1.27</td>
<td>1.14</td>
</tr>
<tr>
<td>.8</td>
<td>12.5</td>
<td>1.30</td>
<td>1.04</td>
</tr>
<tr>
<td>.5</td>
<td>20.0</td>
<td>1.48</td>
<td>.74</td>
</tr>
<tr>
<td>.1</td>
<td>100.0</td>
<td>1.95</td>
<td>.20</td>
</tr>
</tbody>
</table>

Here $G_y$ is a maximum when $q = 1$, and falls rapidly as $q$ falls. In the other particular cases studied, $G_y$ was always a maximum when $q = 1$.

An attempt was made to get a general solution for this property of $q$. Robertson has shown that for $K/a > 5$, a proportionate increase in $K/a$ gives the same arithmetic increase in $\Delta G_{\text{max}}$. At $q = 1$, $G_y \text{ max} = \frac{1}{2} \cdot \Delta G_{\text{max}}$. Since $K/a = \frac{Nn}{Na} \cdot \frac{1}{q}$, $K/a$ will increase proportionately by $1/q$ if $q \neq 1$, and $\Delta G_{\text{max}}$ will increase by $-\log q$. 
Hence \( G_y \max = \frac{1}{2} (\Delta G \max - \log q) q \),

\[
q \neq 1, \quad q = 1
\]

\( G_y \max \) will be \( G_y \max \), if \( \Delta G \max > q(\Delta G \max - \log q) \)

\[
q = 1, \quad q \neq 1, \quad q = 1, \quad q = 1
\]

i.e., if \( \Delta G \max > \frac{q \log q}{1 - q} \).

For values of \( q \) of \( .9, .8, .5 \) and \( .1 \) this function of \( q \) takes values \( .41, .39, .30 \) and \( .11 \) respectively. When \( K/a > 5 \), \( G \max = \frac{1}{C} \frac{z}{p} \sqrt{\frac{p + a}{K}} \) is greater than this function of \( q \), for when \( 1/C \) is small, making \( G_y \) small, \( a \) will be large and \( K/a \) will be less than 5. Thus the maximum value of \( G_y \) when \( K/a > 5 \) will be at \( q = 1 \). The maximum value of \( G_y \) if \( K/a \leq 5 \) also appears to be when \( q = 1 \), except when \( p > \frac{1}{2} \). In such cases the value of \( q \) which makes \( p \) equal to \( \frac{1}{2} \) gives the maximum \( G_y \). However under these conditions \( G_y \max \) will be small.

The nucleus system of testing

In the nucleus system of testing only nucleus breeders may test their stock. It will be assumed there are regulations for all of them to participate and facilities for them to do so. After \( y \) generations of testing the mean of a tested population was shown to be \( \frac{1}{2} \Delta G_q \). In the nucleus system of testing \( q = 1 \), since all sires will be selected on test results and the mean after \( y \) generations \( (H_y) \) will be \( \frac{1}{2} \Delta G \). Let \( d \) be the proportion of multiplier herds using sires from nucleus herds. Then the mean of the multiplier herds in the
What value of \( d \) will maximize \( M_{y+1} \)? There seems no simple solution to this question except for some specific case. It is convenient to consider \( d = 1 \) since the size of the nucleus breeding group can be adjusted to provide all the sires required by the multiplier group. At \( d = 1 \)

\[
M_{y+1} = \frac{1}{2} \Delta G \left[ \frac{y}{2} + \frac{(y-1)}{4} + \frac{(y-2)}{8} + \ldots \right] - \frac{1}{2} \frac{2}{3} \frac{3}{4} \frac{4}{5} \ldots \] 

\[= \frac{1}{2} \Delta G (y-1) \text{ (approximately)}.\]

The testing scheme which will maximize \( \Delta G \), will in turn maximize \( M_y \) at \( d = 1 \).

It is now possible to compare the efficiencies of the open and nucleus systems of testing. In the open system the mean of the pedigree population was shown to be a maximum for most conditions when \( q = 1 \). After \( y \) generations the mean of the pedigree population is \( G_y = \frac{1}{2} \Delta G' y \) in the open system of testing and \( M_y = \frac{1}{2} \Delta G'' (y-2) \) in the nucleus system, where \( \Delta G' \) and \( \Delta G'' \) are the genetic improvements per generation in the respective systems. If \( W \) sires are required on the
basis of the test in the open system, \( W/n' \) sires where \( n' \) is the number of sons a selected boar will sire, will be required in the nucleus system. Thus \( K/a = Nn/Wa \) in the open system and equals \( Nnn'/Wa \) in the nucleus system. Again using the relationship that a proportionate increase in \( K/a \) gives an arithmetic increase in \( \Delta G_{\text{max}} \) for \( K/a > 5 \) then,

\[
\Delta G''_{\text{max}} = \Delta G'_{\text{max}} + \log n'.
\]

In swine \( n' \) will be about 50, whence \( \log n' = 1.7 \). The nucleus system of breeding will be superior to the open system when

\[
\frac{y-2}{2} [\Delta G'_{\text{max}} + 1.7] > \frac{y}{2} \Delta G'_{\text{max}}, \text{ i.e., when}
\]

\[
(y-2) \cdot 85 \gamma_{\Delta G'_{\text{max}}}. \text{ Irrespective of the size of} \Delta G'_{\text{max}},
\]

\[
(y-2) \cdot 85 \text{ can be made to exceed it, showing that eventually the nucleus system of testing will surpass the open system.}
\]

In practice \( \Delta G'_{\text{max}} \) will never be very large unless \( W \) is very small and it is safe to conclude that the nucleus system of testing will yield an improvement superior to that from the open system after four or five generations of testing. The delay in passing on the improvement to the general population is more than offset by the extra gains in the nucleus group. It is likely that the same holds true when \( K/a \) is less than 5. The development and accumulation of improvement in a small nucleus group, with a regular plan for passing it on to the whole breeding group seems to be the optimum method for utilization of testing facilities.
If all commercial sires are bought from pedigree herds, the mean of the commercial population \(C_y\) after \(y\) generations of testing will be \(C_y = \Delta G' \frac{y-1}{2}\) in an open system of testing and \(C_y = \Delta G'' \frac{y-3}{2}\) in a nucleus system of testing, where \(\Delta G'\) and \(\Delta G''\) are the respective genetic gains per generation. That is, the mean of the commercial population will be equal to the mean of the pedigree population in the preceding generation.

The above properties of the different testing systems can be easily demonstrated in any particular situation. The following example compares the open and the nucleus systems of testing in their ability to improve a pedigree population of 1000 herds with testing facilities \(N\) of 1000, 5000 and 100. As it may not be always possible to get \(q = 1\) or \(d = 1\) under practical conditions, the effects of these quantities being less than unity are examined.

With 1000 pedigree herds, the number of sires \(W\) required on the basis of the test is, say 1000. Each sire can produce 50 sons \(nT\) per year. Selection will include both the individuals tested and their relatives (case 2), testing and selection being either on full-sib families of four \((t = 0.3)\) or half-sib families of 40 \((t = 0.1)\). Taking in turn \(N\) equal to 1000, 5000 and 100 and \(q = d = 1\), the genetic improvement per generation in the open system \(\Delta G'_\text{max}\) and in
the nucleus system \( \Delta G^m_{\text{max}} \) can be found from Table 4. Hence \( G_y \) and \( M_y \), the means of the pedigree population after testing \( y \) generations by the respective systems, were evaluated and are shown in Table 9. These results confirm that the nucleus system of testing will exceed the open system in improvement after three to five generations.

The extent of the improvement possible for different values of \( q \) in the open system of testing is of interest since it is unlikely in practice that \( q \) will equal one. In the above example the genetic improvement obtained per generation for values of \( q \) of 1, .9, .8, .5 and .1 have been calculated and are shown in Table 10. In each case the genetic improvement was a maximum at \( q = 1 \), and decreased as \( q \) decreased. Even for values of \( K/A \) less than 5, as in \( N = 100, q = 1 \) gave maximum genetic improvement. At \( q = .9 \) the improvement had fallen off by less than 10%, at \( q = .5 \) by more than 30% and at \( q = .1 \) by over 75%, the decrease being less if \( \Delta G' \) was small at \( q = 1 \).

It is possible to make \( d = 1 \) by adjusting the number of nucleus group herds accordingly. However, if breeders lower in the pedigree scale refuse to use sires from nucleus herds, \( d \) can be less than one. It is of interest to know how the value of \( d \) will affect the genetic improvement. In the same example the improvement after six generations of testing was
Table 9. The improvement possible by the open \((G_G)\) and the nucleus \((M)\) systems of testing at three levels of \(N\), \((W = 1000)\); further description in text

<table>
<thead>
<tr>
<th>(N)</th>
<th>Open testing ((q=1))</th>
<th>Nucleus testing ((d=1))</th>
</tr>
</thead>
<tbody>
<tr>
<td>(N/W)</td>
<td>(\Delta G''_{\text{max}})</td>
<td>(\Delta G''_{\text{max}})</td>
</tr>
<tr>
<td>1000</td>
<td>(.85 \sigma_G) (at (m=5, t=.1))</td>
<td>(50)</td>
</tr>
<tr>
<td>(G_1)</td>
<td>(.43 \sigma_G)</td>
<td>(G_1)</td>
</tr>
<tr>
<td>(G_2)</td>
<td>(.85 \sigma_G)</td>
<td>(G_2)</td>
</tr>
<tr>
<td>(G_3)</td>
<td>(1.28 \sigma_G)</td>
<td>(G_3)</td>
</tr>
<tr>
<td>(G_4)</td>
<td>(1.70 \sigma_G)</td>
<td>(G_4)</td>
</tr>
<tr>
<td>5000</td>
<td>(1.36 \sigma_G) (at (m=2, t=.3))</td>
<td>(250)</td>
</tr>
<tr>
<td>(G_4)</td>
<td>(2.72 \sigma_G)</td>
<td>(G_4)</td>
</tr>
<tr>
<td>(G_5)</td>
<td>(3.40 \sigma_G)</td>
<td>(G_5)</td>
</tr>
<tr>
<td>100</td>
<td>(.34 \sigma_G) (at (m=1, t=1))</td>
<td>(1.30 \sigma_G) (at (m=2, t=.3))</td>
</tr>
<tr>
<td>(G_6)</td>
<td>(.34 \sigma_G)</td>
<td>(G_6)</td>
</tr>
<tr>
<td>(G_7)</td>
<td>(.51 \sigma_G)</td>
<td>(G_7)</td>
</tr>
<tr>
<td>(G_8)</td>
<td>(.68 \sigma_G)</td>
<td>(G_8)</td>
</tr>
</tbody>
</table>

Table 10. The genetic gains \((\Delta G' = \Delta G_{\text{max}}q)\) possible by the open system of testing for 3 values of \(N\), and a range of values of \(q\) \((W = 1000)\)

<table>
<thead>
<tr>
<th>(q)</th>
<th>(1000)</th>
<th>(5000)</th>
<th>(100)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(.85 \sigma_G)</td>
<td>(.36 \sigma_G)</td>
<td>(.34 \sigma_G)</td>
</tr>
<tr>
<td>(.9)</td>
<td>(.75 \sigma_G)</td>
<td>(.27 \sigma_G)</td>
<td>(.32 \sigma_G)</td>
</tr>
<tr>
<td>(.8)</td>
<td>(.71 \sigma_G)</td>
<td>(.16 \sigma_G)</td>
<td>(.30 \sigma_G)</td>
</tr>
<tr>
<td>(.5)</td>
<td>(.52 \sigma_G)</td>
<td>(.82 \sigma_G)</td>
<td>(.23 \sigma_G)</td>
</tr>
<tr>
<td>(.1)</td>
<td>(.12 \sigma_G)</td>
<td>(.21 \sigma_G)</td>
<td>(.08 \sigma_G)</td>
</tr>
</tbody>
</table>
Table 11. The means of the pedigree population ($M_n$) after six generations of a nucleus system of testing for 3 values of $N$ and a range in values of $d (W=1000)$

<table>
<thead>
<tr>
<th>$d$</th>
<th>1000</th>
<th>5000</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.38 $h \sigma_G$</td>
<td>5.40 $h \sigma_G$</td>
<td>2.60 $h \sigma_G$</td>
</tr>
<tr>
<td>.9</td>
<td>4.31 $&quot;$</td>
<td>5.25 $&quot;$</td>
<td>2.54 $&quot;$</td>
</tr>
<tr>
<td>.8</td>
<td>4.15 $&quot;$</td>
<td>4.98 $&quot;$</td>
<td>2.47 $&quot;$</td>
</tr>
<tr>
<td>.5</td>
<td>3.29 $&quot;$</td>
<td>3.94 $&quot;$</td>
<td>2.07 $&quot;$</td>
</tr>
<tr>
<td>.1</td>
<td>1.93 $&quot;$</td>
<td>1.15 $&quot;$</td>
<td>.62 $&quot;$</td>
</tr>
</tbody>
</table>

computed for values of $d$ from 1 to .1. It is apparent from the results, shown in Table 11, that the genetic improvement was decreased if $d < 1$. At $d = .5$ the improvement had fallen off by over 20%, and at $d = .1$ by over 75%.

The maximum improvement from an open system of testing is obtained when all the pedigree breeding herds can use sires selected on the basis of the test. If the number tested ($N$) is small compared with the above requirement, the improvement expected can only be small. A more efficient system of testing is one which tests animals only from nucleus herds, accumulates the improvement in these and systematically passes it down to the multiplier-pedigree breeders in the following generation. Again improvement will be a maximum when all pedigree breeders can purchase sons of selected sires, i.e. $d = 1$. The size of the nucleus group can be recommended to fit this requirement.
The progeny test

In the progeny test proper, selection is made among parents on the basis of their offspring's performance as to which parents will see further use and will sire the future breeding animals. On the other hand, selection of young sires and dams because their parents had a good progeny test is really selection on sib performance.

To be effective the progeny test must compensate for the longer generation interval incurred, by increasing the accuracy of selection. In swine the generation interval is short. Consider the character rate of gain in the diagram below.

<table>
<thead>
<tr>
<th>0</th>
<th>6 months</th>
<th>1 year</th>
<th>1 1/2 years</th>
<th>2 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth</td>
<td>Sexually mature</td>
<td>Offspring</td>
<td>Offspring performance</td>
<td>Offspring performance - Basis of parent selection</td>
</tr>
<tr>
<td>Own performance</td>
<td>Sib performance</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Selection for rate of gain on own performance or sib performance is possible at six months of age giving a generation interval of one year. Selection of parents on offspring performance is possible at 18 months and the generation interval is two years. The length of the generation interval is
thus doubled by a progeny test. For other traits such as body length, back-fat probe and feed efficiency, all of which are directly measurable on the breeding animals, the generation interval is doubled by the progeny test. For carcass traits, sib performance is available at six months and progeny data at 18 months. For traits of sow productivity, individual records are available at 12 months and the progeny records at 24 months.

In swine many of the important production traits can be measured directly on the males, as contrasted with egg production and milk production which are measurable only on the females of the respective species. Furthermore, the heritabilities of economic traits in swine are comparatively high. For example, carcass traits have heritabilities near .5, and rate and efficiency of gain around .25. Hence it seems doubtful that the added accuracy in selection made possible by the progeny test would outweigh the increase in the generation interval sufficiently to justify the use of more than a small fraction of progeny tested males.

In a closed herd of 20 sows, Dickerson and Hazel (1944a) showed that the supplementary use of the progeny test will reduce the improvement possible by individual selection for characters with heritability of .125 or greater. For carcass traits, supplementary culling on progeny performance after
initial selection on sib records failed to increase the genetic gain at a heritability of .5, and did not increase it appreciably when the heritability was as low as .1. Although shown for only certain particular cases, it would seem that the above findings apply widely and to all sizes of herds and to most economic characters.

Robertson and Rendel (1950), in a herd of 120 dairy cattle, found only a slight advantage in progeny testing over individual selection for butterfat production, while Dickerson and Hazel (1944a) found in the same example, that the extensive use of progeny tested sires would slightly reduce improvement. However, Robertson and Rendel (1950) have shown that the progeny test may indeed give substantial gains in an artificial insemination unit of 2000 cows and that the gain increased as the size of the unit increased. In view of the finding it is conceivable that progeny testing may be also worthwhile in testing schemes in swine.

Testing facilities are best used by testing animals from the nucleus breeding herds. Because of the high reproductive rate in swine this nucleus group can be comparatively small. Hagedoorn (1948) advocated a small progeny-tested nucleus group of ten sires, with all breeding operations based on them and their sons in a commercial population of 150,000 sows. In such a scheme, the accuracy in evaluation of the
chosen sires would be important and perhaps the use of the progeny test would be worthwhile. An example of such a scheme can be considered and the efficiency of various systems of testing compared.

Suppose ten sires are required per generation, and 1000 animals can be tested. The improvement from selection on individual performance will be $2.67 \sigma_G$ for the selected males, and $1.33 \sigma_G$ for all breeding animals if no selection is practiced on the females. At the high values of $N/T$ in such problems, (here $N/T = 100$), mass selection will be more effective than selection which includes relatives at home (case 2). Selection on a test group basis will be more effective than individual selection only if $t$ is much smaller than $r$.

A more efficient basis for individual selection is an index combining own performance with that of $m$ relatives. Lush (1947) has shown that the efficiency of the latter to selection on own performance alone is

$$\frac{\sqrt{1 + (r-t)^2 (m-1)}}{(l-t) l+(m-1)t}.$$ 

Since values of $t$ will rarely exceed .5 in swine testing, it can be seen from Figure 5 of Lush (1947) that only for high $r$'s and low $t$'s will selection on such an index be worthwhile. This corresponds to cases where individual se-
lection is inaccurate and the additional records on sibs
greatly increase the information on any individual.

Improvement effected by the progeny test proper can
be found by the method of Robertson (1957) earlier described.
Here $K = N/S = 100$. For values of $t$ of .4, .3, .2, .1 and .05
the maximum genetic superiority ($\Delta G_{\text{max}}$) of the selected
sires is, respectively, 1.46 h\(\sigma\), 1.52 h\(\sigma\), 1.69 h\(\sigma\),
2.01 h\(\sigma\) and 2.28 h\(\sigma\). Since the progeny test doubles the
generation interval in the males the annual genetic gain
from progeny testing is $\Delta G_{\text{max}}/(3)$. In the above cases this
is always less than that from individual selection.

The use of the progeny test as a supplement to earlier
selection on own performance can be studied using the formulae
of Dickerson and Hazel (1944a). Suppose the 50 best indi­
viduals of 500 tested are selected, each survivor progeny
tested on ten offspring, and the best ten sires finally chosen.
The progress from initial selection of the males ($\Delta S_1$) =
1.76 h\(\sigma\) and the further improvement on progeny testing
($\Delta S_2$) = 1.37 h\(\sigma\) ($G = .30$ $L = .20$). The annual improve­
ment where half of the males used are progeny tested is
.98 h\(\sigma\). Under the same plan where $G = .125$, $L = .25$ and
$E = .625$ the annual improvement would be 1.05 h\(\sigma\). If the
initial 50 were selected from 750 tested and then tested on
five offspring each, the annual improvement for the above
values of G etc. would be slightly less in both cases. Improvement in the above cases was always less than that from individual selection.

In traits which can be measured only on the carcass, selection on collateral relatives is possible. The information given by the sib test is very similar to that given by the progeny test. The value of the full-sib test is limited by the intra group correlation (t) being large and the test group size (m) being small. In the half-sib test, the genetic relationship of .25 is half of that found in full sib and progeny tests. In general, these limitations on the full-sib and half-sib tests are not as serious as is the increased generation interval of the progeny test. For the above example, a full-sib test was more efficient than either the progeny test alone, or initial selection on sib performance and further selection on progeny records.

If an accurate measure of the carcass traits can be made on the live animal, greater improvement may be achieved by direct selection on this measurement than by indirect selection on sib carcass measurements. For example, the backfat probe has been developed to measure the backfat thickness on the live hog (Hazel and Kline 1952).

Selection on own performance seems most suitable in effecting improvement for most economics traits in swine test-
ing. Where $t$, the intra test group correlation, is low, the additional use of sib information is worthwhile. On the basis of the above examples, the role of the progeny test, where it might be appropriate, is more successfully replaced by the sib-test. In swine, the records on most characters are available concurrently with sexual maturity. The retention of large numbers of unproductive males until sib test records are available, as in dairy cattle and poultry, is not necessary in swine. For carcass traits, sib-tests are recommended but if some method of measuring carcass quality in the live animal is available, individual selection may be more efficient.

**Testing on the farm**

In the preceding sections the theory and the examples have dealt with the improvement expected from testing swine under different test schemes at a central testing station. Testing can also be carried out on the farm and selections made within the herd.

On a farm, facilities for elaborate test techniques will be lacking because of the expense and labor they entail. However, in swine, several traits can be measured readily and without much additional work or expense. These may respond well to testing and selection within the farm. For example, weight for age and backfat probe each involve only
one measurement taken at slaughter weight. Furthermore, correction factors have been developed to convert weight to a standard age, and backfat probe to a standard weight, so that the records can be taken on relatively large groups of animals and then standardized to eliminate major differences in age and weight. Some traits such as sow productivity are more conveniently measured on the farm, while others such as feed efficiency are likely to require more facilities and labor than the breeder is prepared to give.

Consider selection for weight-for-age in a two-sire herd of 20-30 sows. There will be about 80 males and 80 females available for selection at six months of age. Selection shall be of the best two males from different litters \( (p = 4/80, z/p = 2.06) \) and of the best 20 gilts \( (p = 20/80, z/p = 1.27) \). An annual improvement of \( 1.7 h\sigma_G \) would be expected. Breeding the young boars from the best gilts (say the best four) would decrease the selection differential for boars in the next generation and lower the annual genetic gain over two years to \( 1.4 h\sigma_G \).

Selection may be on the average performance of the whole litter, the best male and all females of the best litters being selected. The genetic superiority of the selected males, \( \Delta G_m = h\sigma_G \left[ \frac{z_1}{P_1} \frac{1+(m-1)r}{m} \sqrt{\frac{m}{1+(m-1)t}} + \frac{z_2}{P_2} \frac{1-r}{1-t} \right] \)
where $p_1 = 2/20$, $p_2 = 1/4$, $r = .5$, $m = 8$. For values of $t$ of .3, .2 and .1 respectively, $\Delta G_m$ is 2.10 $h\sigma_G$, 2.23 $h\sigma_G$, and 2.38 $h\sigma_G$. The genetic superiority of the selected gilts

$$\Delta G_T = \frac{Z}{p} \cdot h\sigma_G \frac{1+(m-1)t}{m} \sqrt{\frac{m}{1+(m-1)t}}$$

where $p = 5/20$ and $r$, $m$ and $t$ are as before. The annual genetic improvement in the herd from such selection is 1.60 $h\sigma_G$, 1.74 $h\sigma_G$, and 1.89 $h\sigma_G$ for values of $t$ of .3, .2 and .1, respectively. When $t$ is low, selection on the basis of litter performance is more efficient than on individual performance, and vice versa if $t$ is high. Since only two sires are used per herd, selection on a sire basis will reduce improvement unless $t$ is very low. Osborne (1957) has presented graphs and formulae showing when the use of sire and dam family averages increase the efficiency of selection under a hierarchical mating system.

For carcass traits, selection may be based on sib performance. Fredeen (1954) has shown that slaughter of a test group of two or three males per litter will give maximum genetic gains within a farm. However it is unlikely that any breeder would follow this program as his income is largely dependent on the sale of young boars. A slaughter group of two gilts per litter would seem more practical. Suppose one male from each of the best two litters, and the remaining two gilts from the best ten litters are selected. This scheme
would yield about 75% of the improvement in carcass qualities of that proposed by Fredeen and yet leave all the males for sale for breeding purposes. Fredeen (1954) has shown that if some live measure is a reliable indicator of carcass merit selection on this measure may increase the improvement by as much as 30%.

Although differences in environment and other farm effects may exist between farms, these will be common to all pigs within each farm. Hence selection on the basis of deviations from the farm mean is valid, irrespective of the level of husbandry. In this way it would appear that substantial improvement could be brought about by testing on the farm. In an average farm an improvement from $1.5 \sigma_G$ to $2.0 \sigma_G$ could be achieved in traits measured directly on the live animal and from $.5 \sigma_G$ to $1.0 \sigma_G$ for carcass traits. The central testing station will have to better these gains if it is to be worthwhile. Testing on the farm and testing at a central testing station are not mutually exclusive, but can be made to supplement each other. The use of testing at both levels is likely to achieve greater improvement than that by either one alone.

The existence of herd differences in genetic merit are not brought out by testing on the farm since genetic merit is confounded with the level of husbandry. In farm testing,
each breeder can improve his stock a little, while in a central station, stocks of superior merit can be identified and quickly spread over the whole population. It is as if instead of each breeder on the breeding ladder moving up one step, all are lifted to near the top step. In testing on the farm, the relevant variation and heritability in estimating improvement will be those within a stock within a farm. At the testing station, the relevant variation and heritability will be over all stocks, and over all carry-over effects of farm differences. Sutherland (1958) found that farm effects were unimportant in the test performance of unrelated test groups from the same farms in different seasons. If differences between stocks in test performance are largely genetic, a central testing system will be much superior to a farm test. Most pedigree breeders maintain only one breed of stock. Breed characteristics will not be brought out by farm testing, while they will be made apparent at a central testing station.

If selection is confined to animals within the herd, the breeder is soon confronted with the problem of inbreeding. After four generations of a closed two-sire herd the inbreeding coefficient is near 25% and increases steadily thereafter. This difficulty can be overcome in practice by cooperating in a breeding plan with other breeders and exchanging breeding animals, or by mating sons of one boar in a herd to the daugh-
ter of the other boar. This latter plan reduces the rate of inbreeding almost by half.

Selection on several traits

Only in special cases in animal improvement can all the potential for selection be applied to one trait. Generally several economic traits will be improved concurrently. Hazel and Lush (1943) have shown the method of selection on an index combining several traits to be more efficient than those of independent culling levels or tandem selection. The traits to be improved are not likely to be independent and changes in one trait may bring changes in the others. The derivation of an index weighting each trait according to its heritability, its economic importance and its relationship with other traits was given by Smith (1937) and Hazel (1943).

The aggregate genotype of an individual \( H \) may be expressed as \( H = \sum_{i} a_{i} G_{i} \) where \( G_{i} \) are the genotypes and \( a_{i} \) the economic values of the traits being considered. The \( G_{i} \) cannot be measured but the phenotypic traits \( (X_{i}) \) can be measured. The selection index \( I = \sum b_{i} X_{i} \) where the \( b_{i} \) are chosen such that \( R_{HI} \) is a maximum. The \( X_{i} \) need not correspond to the \( G_{i} \).

The normal equations from maximizing \( R_{HI} \) are
\[ \sum \sum b_i \text{Cov } X_i X_j = \sum \text{Cov } X_i X = \sum \sum a_i \text{Cov } G_i G_j. \]

To find the \( b_i \)'s the set of simultaneous equations must be solved.

The improvement from selection on an index \( I \) is

\[ \Delta G = \frac{2}{p} b_{HI} \mathcal{O}_{I}, \text{ but } b_{HI} = 1 \text{ by definition} \]

\[ = \frac{2}{p} \mathcal{O}_{I}. \]

Hence improvement is proportional to \( \mathcal{O}_{I} \), and the size of \( \mathcal{O}_{I} \) is a basis for comparing the efficiencies of different indexes in selection.

Changes in group size, in correlations within the groups and in the traits being considered all will alter the set of simultaneous equations and new solutions for the \( b_i \)'s will be necessary at each change. Hence solutions to determine the optimum group size, the improvement at different values of \( t \) and \( n \), and so on, or in other words, to compare the efficiencies of different testing schemes, will not be simple to obtain especially if many traits are included in the index. Hazel (1943) and Legates (1949) have computed the index coefficients (\( b_i \)'s) for the indexes with which they were working for different numbers of records per animal, and different numbers of relatives available. Such work may be greatly reduced by the use of electronic computers to solve the equations for the \( b_i \)'s.
The following calculations were made to examine the increase in efficiency of selection if individual feeding were to replace group feeding at the Iowa swine testing station. Sutherland (1958) found an aggregate genotype for current Iowa conditions as

\[
H = 2.00 \, G_1 - 6.00 \, G_2 - 0.00 \, G_3 + 0.35 \, G_4
\]

where \( G_1, G_2, G_3 \) and \( G_4 \) respectively represent daily gain, efficiency of gain, backfat probe and percent lean cuts. The phenotypic variance and co-variances obtained by Sutherland (1958) were changed to these which would apply if individual feeding was practiced. Thus the variance of individual efficiency of gain \( \sigma^2_Y = \frac{m \cdot \overline{VE}}{1 + (m-1) \cdot t}, \quad (t = .25) \) and the covariance of backfat probe (\( P \)) and individual efficiency of gain \( \text{Cov.} \, PE = m \cdot \text{Cov.} \, \overline{PE} - (m-1) \cdot r \cdot \text{Cov.} \, G_pG_e \) \( (r = .35) \) and similarly for rate of gain.

The index obtained for selection on individual feeding is \( I_1 = 1.77 \, X_1 - 7.94 \, X_2 - 2.69 \, X_3 \) and \( \sigma_{I_1} = 1.58 \) where \( X_1, X_2 \) and \( X_3 \) respectively are daily gain, individual efficiency of gain, and backfat probe. Under group feeding, Sutherland obtained the index \( I_2 = 2.90 \, X_1 - 7.71 \, X_2 - 3.63 \, X_3 \) and \( \sigma_{I_2} = 1.38 \). Thus records on individual feed efficiency will increase the accuracy of selection by about 15\%.

Jonsson (1957) has shown in Danish tests that the variation in daily gain was markedly reduced under individual feeding and the correla-
tion between litter mates was increased as compared with group feeding. How the variance and covariance components for rate of gain and other traits would be altered in the above example is not known.

Assuming the selection differential is unchanged by substituting individual feeding for group feeding, the improvement affected by selection on the indexes and on the individual traits is compared below in Table 12. The high economic value and high heritability of feed efficiency make it a dominant factor in the index and in improvement.

Table 12. Relative improvement from selection on different criteria

<table>
<thead>
<tr>
<th>Selection on</th>
<th>Improvement—(units of H)/z/p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Index 1</td>
<td>1.58</td>
</tr>
<tr>
<td>Indiv. Effic.</td>
<td>1.52</td>
</tr>
<tr>
<td>Index 2</td>
<td>1.38</td>
</tr>
<tr>
<td>Group effic.</td>
<td>1.19</td>
</tr>
<tr>
<td>Backfat probe</td>
<td>.77</td>
</tr>
<tr>
<td>Daily gain</td>
<td>.71</td>
</tr>
</tbody>
</table>

The extra facilities and labor required for individual feeding will reduce the number of animals that can be tested.
by about half. If 400 can be tested when group fed and 200 when individually fed, the improvement from individual feeding will only be greater if less than ten animals are selected. The reduction in the selection differential if more are selected is not offset by the greater accuracy of selection. Since about 200 animals are selected on test results, group feeding is more efficient in this testing scheme than is individual feeding.
DISCUSSION

Attention has been focused recently on the use of the central testing station as a means for seed-stock evaluation and of increasing the rate of genetic improvement in farm animals. To ascertain the worth of testing schemes requires firstly some method to determine the optimum testing procedure, secondly some knowledge as to how a testing system can fit best into the population, and thirdly a basis for comparing the improvement made with that possible by other plans.

The factors affecting improvement by selection on test results can be divided arbitrarily into two categories. The one would encompass the broad aspects of testing, such as the resources available, the numbers required for breeding, the application of test results and the biological properties of the species. The other would include the details of the test such as the type of testing, the test group number, the testing environment and other particulars which can be manipulated to maximize the efficiency of the test. Most of the studies in the past have been more concerned with the latter, namely of deriving the optimum testing procedure under specified conditions. However, apparently of more significance in improvement are the broad aspects of testing, and although their manipulation will be more difficult, it may be correspondingly more rewarding.
Any system of testing will incur extra expenses over standard production costs in the form of housing, measuring and evaluating the animals being tested. The size of the test will depend on the resources available in terms of capital but not directly so. The cost of testing can be varied according to the accuracy of the measurements, the elaborateness of housing and facilities and the extent of recording and analyzing the data. Thus for fixed capital investment, the number of animals tested can be varied according to the accuracy of the evaluation of each.

The improvement will be greater as the resources increase. Other things being constant, the improvement will be roughly proportional to \( \log N \), where \( N \) is the number of animals tested. When \( N \) is initially large, only impractically large \( N \)'s can yield further substantial improvement. After a certain point, the resources may be better used to some other end. Where liberal government spending is allowed, such cases may arise. The improvement per unit of input, say per tested animal, although it is not a good criterion of efficiency, will decrease as \( N \) increases. It will be a maximum for any \( N \) when the number required for breeding \( (T) = N/2 \) and \( p = \frac{1}{2} \).

The sufficiency of the number tested is relative to the size of the population to be improved or more specifically to its breeding fraction. The latter may be considered at one
of three levels, namely that of the whole population, of the pedigree herds or of a small elite group of herds. In Iowa, for example, there are from 150,000 to 180,000 boars being used, from 2000 to 3000 of these in pedigree herds and some 50 to 100 in the top nucleus herds, if such can be said to exist. The difference in numbers in the three groups is revealing. The size of the population and its breeding structure are seen to be relevant in livestock improvement. The phase at which a testing scheme can be best applied and its results most suitably used has great significance.

The annual improvement from selection is likely to be small, but it can be accumulated steadily over several generations by the use of a wise breeding scheme. If tested males are used to sire commercial stock, the effects of any improvement is lost when the stock is sold. On the other hand, improvement can be accumulated in the nucleus pedigree herds and later passed on to the rest of the population.

Considering the testing scheme as the sole source of improvement, several points can be made. If the number of animals tested is few, the improvement obtained can only be small. The maximum improvement will always come when all pedigree breeders can use sires bearing a high relationship to selected stocks. The less that this is possible, the less the improvement will be. The most efficient system of testing
and breeding requires that only animals from the elite nucleus herds be tested. In this way, the resources will be more nearly sufficient for accurate evaluation of the selected animals and will permit greater choice in selection. The delay in passing on the improvement to the general population is more than offset by the extra gains in the nucleus group.

The different roles a testing system can play in a swine improvement program are well demonstrated by comparing the organization of the swine breeding programs in Denmark and Iowa. In Denmark there are three central testing stations testing pigs from 250 state-approved breeding centers, with supplementary testing and breeding units. The 250 breeding centers form an elite nucleus breeding group and are under regulations as to the numbers to test and the level of excellence. The breeding centers are thus in intimate contact with the testing stations and base their selections to a greater or less degree on the results of the tests. In Iowa, on the other hand, there is no differentiation between pedigree breeders and each breeder has an equal chance to use the testing facilities, but is under no compulsion to do so. As yet the facilities are limited and only about 10% of the breeders are able to test entries. Many of the tested animals and their relatives are sold to commercial producers. Breeders are completely free to buy their herd sires from out-of-state
herds or from non-testing breeders. The test results, therefore, figure but little in the selection of pedigree herd sires and consequently can have little part in improvement. In Denmark the testing system is an integral and paramount part of the swine improvement program, while in Iowa it is only a subsidiary item competing with other improvement plans. Fredeen (1954) has shown virtually no improvement after more than twenty years of testing in Canada. The reason for this, he concludes, is that the results of testing have not been used in making selections of breeding stock. Testing will be futile unless the results are used as a basis for selecting breeding stock.

The rate of improvement will also depend on such quantities as the generation interval and reproductive rate of the species. In swine the combination of a high reproductive rate, short generation interval and high heritabilities make the possible improvement from testing and selection in swine quite appreciable. Again the economic traits in swine are measurable early and in both sexes, as contrasted with other species such as dairy cattle. These considerations make the performance test of individuals and their resultant selection the most promising method of swine improvement.

The optimum test is the one which fits best under the broader specifications of numbers tested, the numbers required
for breeding, the breeding structure of the population, the biological properties of the species and so on. The testing procedure can be more readily varied than these broader aspects of the population. There are methods to determine the optimum combination of the variables in testing especially with regard to the type of test, the size and composition of the test group and correlations between the test animals. Finding the optimum structure of the test is comparable to finding the best adjustment of a measuring tool in a quantitative experiment.

There are many important aspects in determining the efficiency of testing schemes which have not been considered here. Of special concern are the non-random persistent effects which bias evaluation. Part of the reason for testing under standard conditions is to reduce the more important of these. Thus at a central testing station, the influence of farm environment, the greatest single factor affecting performance, is standardized. Removing this source of variation causes other sources to become relatively more important. The performance of each animal is the result of the interplay of its genetic make-up on an environment. Non-random variations in the latter will bias the evaluation. Such are caused by persistent farm and maternal effects, different procedures in selecting the test groups sent to the station and by pen and minor differences within the station. Furthermore, the
accuracy of evaluation is further reduced if heredity environmental interactions exist, so that different stocks perform differently under different environments. Important questions as regards the efficiency of testing are how large are these sources of variation relative to the genetic variation and what can be done to reduce them.

The improvement that has been considered is that resulting from some process of testing and selection. This will be largely dependent on the portion of the total variation that is genetic, and more specifically on the fraction of the genetic variation that is additive. Variations caused by dominance and epistasis are not inherited as such since the gene combinations which cause them are partly or wholly broken up on segregation and recombination. Thus the gains from selection are dependent on the additive genetic variance, and if this is small the improvement will also be small. There are also breeding plans to take advantage of non-additive genetic variation. The central testing station can be a useful tool in effecting improvement by such schemes. Comparisons can be made of different crosses and hybrids, and the parents selected on the performance of their crosses. The random sample tests in poultry are examples of such a case, many breeders presumably conducting similar tests within their own flocks. The comparisons among the breeder stocks are valuable both to the breeders and to the commercial producer.
There are many other considerations which, though non-genetic themselves, can play a very important part in effecting genetic improvement in the population. In testing work the value of such abstract matters as public opinion, education, standards of excellence and demonstration of techniques may be difficult to measure and yet play a fundamental part in effecting improvement.

The results from a testing station are official and public, and are available for all to study and compare. The propaganda and sales talk so common in pedigree breeding circles are offset by a factual report of performance. Indeed the success of the former may be due to the lack of the latter. The comparison between stocks on a common basis is available. Poor stocks are identified and poor breeders forced into attempting to improve their herds. The wish of the breeder to have his animals do well at the station, as this will affect his sales, stimulates efforts at constructive breeding. In turn, those breeders who have or develop superior stocks will be identified and rewarded. Much of the incentives and value of the test can be lost if the results are not made public.

The test gives the breeder a basis for selection within his own herd. It also gives him a sound basis for selecting animals from outside his herd and of introducing superior animals. In this way he can up-grade his herd quickly or make
compensatory matings to correct weaknesses the test or his observations show in his own herd. Similarly the test gives comparisons between breeds and can demonstrate clearly the characteristics of each breed.

The testing station serves as a focal point of improvement. Otherwise each breeder is vague as to the merit of his stock and the success of his breeding policy. As superior stocks are developed, whether by selection or other methods, they are identified, brought before the public and may be widely used. The standards of merit set by the station as regards performance, carcass qualities and appearance, give both the breeder and the commercial producer standards to compare different stocks, and goals to aim at in the future.

The relative stress put on the various traits in evaluation at the station are likely to influence breeders in their selections. Realistic appraisal of the relative economic values of different characters will govern the evaluation at the station. This assessment is likely to be more reliable than that of the individual breeder. However in that the appraisal is not sufficient or is ill-advised, the goals set by the station may lead the breeders far astray. Before any testing system is started much work should be done to enunciate clearly which things are important and ought to be stressed in selection, and continual revision may be necessary if con-
ditions are not stable.

A testing station allows professional animal husbandry-men to come into closer contact with the breeding work. In this way they can exert influence and recommend or demonstrate at first hand more effective methods of feeding and breeding. In turn they will learn to appreciate the problems and viewpoint of the breeder. Control of the testing station either by the breeders or the animal husbandry-men is to be deprecated since control might lead to exploitation by the different interests.

Finally, a testing station gives an excellent opportunity for education in animal husbandry. The demonstration by the test of the principles of good husbandry and housing, and of the unbiased measurement of productive ability is invaluable.

All these points are important in animal improvement although their influence may be hard to measure. Getting the breeder to recognize the goals of improvement, and giving him the tools and a good incentive to effect it, seem more necessary in increasing progress than liberal testing facilities and tests which were neither widely known nor effectively used.
SUMMARY

Extensions have been developed for the method of Robertson (1957) to determine the optimum group size in a progeny test or sib test. These extensions represent three methods of selection in swine, namely selecting tested animals, selecting both tested animals and their relatives, and selecting the relatives only as in a slaughter test. An example comparing the improvement from testing and selection under these three methods has been given, encompassing a wide choice of testing possibilities.

The extent of the improvement is proportional to \( \log \frac{N}{T} \), where \( N \) is the number tested and \( T \) is the number of breeding stock required, and to the heritability of the trait being considered. Further modification of improvement depend on the size and the type of family represented by the test group, and on the intra-group correlations in the test. At large values of \( N/T \) a high accuracy is important in evaluation. Consequently selection of animals actually tested, either as individuals or as groups, is superior in such cases. As \( N/T \) decreases the existence of untested relatives becomes important because fewer animals may be tested than are required. At low values of \( N/T \) the proportion of tested animals among those selected is small, the test group size is small and the overall relationship to tested animals is small (\( r = .25 \)). Under such conditions the
genetic improvement can only be small. The slaughter test will always be less efficient than an individual performance test as the tested animals will be slaughtered and not included among those selected, but at low values of N/T the difference will be small. The larger the family size in any category and the smaller the intra-group correlation at some level at heritability, the greater will be the improvement from testing.

Of perhaps more importance in livestock improvement is how the testing system is integrated with the population structure. If, for example, selected animals are used solely to sire commercial stock no accumulation of merit can occur in the breeding herds. Where any breeder may test entries the maximum improvement will be obtained when all pedigree herds use sires highly related to animals selected on the basis of the test. The less that this is achieved, either by testing insufficient numbers, or by refusal of the breeders to cooperate, the less the improvement from testing will be. The effective size of T, the number required for breeding, can be greatly reduced by considering only a nucleus group of breeders, and using all the testing facilities and opportunity for selection on their stock. This system seems to give maximum improvement when all pedigree breeders use males from this nucleus. When facilities are limited and such a structure exists in the population, this design will give the greatest improvement.
Where the progeny test would be appropriate in swine testing, as for the improvement of carcass traits, it is more successfully replaced by the sib test. Even for carcass traits the efficiency of selection may be increased by having some indicator of carcass merit on the live animal.

Testing on the farm can provide appreciable improvement, for characters easily measured on the farm, and especially in selecting female breeding stock. To be justified the central testing station should surpass the farm test in the rate of improvement it achieves. The two systems should be used to supplement each other, and their combination should further increase improvement.

Where several traits are to be improved concurrently the selection index must be used to combine and weight them properly. The incorporation of the index into these problems concerning efficient schemes of testing is not easy, since even slight changes in the variables require new solutions of the simultaneous equations in finding the coefficients and the variance of the index.

Many other aspects affect the efficiency of testing schemes. Not the least of these are the political and education aspects afforded by the system, and the value of having a planned policy and set goals of improvement.


Osborne, R. 1957. The use of sire and dam family averages in increasing the efficiency of selective breeding under a hierarchical mating system. Heredity, 11:93-118.


