EFFECTIVENESS OF SELECTION ON PROGENY PERFORMANCE AS A SUPPLEMENT TO EARLIER CULLING IN LIVESTOCK

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INTRODUCTION

The extensive literature on the use of the progeny test in selecting breeding animals deals almost exclusively with its accuracy, as compared with that obtained from the use of pedigree, individual performance, or averages of collateral relatives, as an indicator of transmitting ability. Although several investigators, particularly Wright (15) and Lush (3, 4, 5), have emphasized difficulties in the practical use of the progeny test, its accuracy under properly controlled conditions is unquestioned. However, from the standpoint of genetic progress expected from selection in a given period of time, the usefulness of the progeny test is greatly influenced by factors other than its relative accuracy. The most important of these are the age at which progeny tests can be obtained and the rate of reproduction. The longer interval between generations that results from use of the progeny test in selection tends to offset the advantage of more accurate selection and may actually reduce the rate of improvement obtained.

The purpose of this study is to examine the effectiveness of selection based on the progeny test when it is used to supplement earlier selection. The criterion of effectiveness is the average genetic improvement expected yearly from early selection alone as compared with that expected when use is made of the progeny test. The examples have been chosen to include economic traits in farm livestock for which the basis of earlier culling is restricted to individual performance, pedigree, or average performance of collateral relatives.

ANNUAL IMPROVEMENT EXPECTED FROM SELECTION IN CLOSED POPULATIONS

The two factors that determine annual improvement from selection in any closed population are (1) the average genetic superiority of those animals selected to become parents over the group from which they were chosen ($\Delta P$) and (2) the average age of parents when their offspring are born or the average interval between generations ($T$). These averages are weighted according to the proportion of offspring from parents of different sex and age groups. Since $\Delta P$ represents the average genetic gain in $T$ years, the average annual gain is

$$\Delta G = \frac{\Delta P}{T}.$$
The most effective plan of making selections is the one that produces most improvement per unit of time. One plan may be more effective than another because it (1) increases $\Delta P$ and/or decreases $T$, (2) increases $\Delta P$ relatively more than $T$, or (3) decreases $\Delta P$ relatively less than $T$. The effect of changing $\Delta P$ and $T$ is illustrated in figure 1.

The parents of the animals born in any one year differ in age and in the intensity of the selection applied to the different age groups and sexes. When the different parents within each age and sex group have equal opportunity to produce offspring, the average yearly genetic progress expected in two successive cullings of sires and of dams is

$$
\Delta P \text{ for sires} \quad \Delta P \text{ for dams} \quad \Delta G = \frac{N_1\Delta S_1 + N_2(\Delta S_1 + \Delta S_2) + M_1\Delta D_1 + M_2(\Delta D_1 + \Delta D_2)}{N_1Y_1 + N_2Y_2 + M_1Z_1 + M_2Z_2} \quad \frac{T \text{ for sires}}{T \text{ for dams}}
$$

This formula is rigorously proved algebraically from the fact that the average breeding value of an unselected group of offspring tends to be the same as that of the parents and may be extended to any number of successive cullings. The assumption is made that the average difference between offspring born in successive years ($\Delta P$) is constant, as would be expected for polygenic traits in a closed population where a regular breeding plan was in use.
in which

\[ \Delta S_1 = \text{average genetic superiority of young sires retained in the first selection} \]

\[ N_i = \text{proportion of the offspring that are from young sires} \]

\[ Y_1 = \text{average age of young sires when their offspring are born} \]

\[ \Delta S_2 = \text{additional genetic superiority of sires obtained from the second culling of sires retained in the first selection} \]

\[ N_2 = \text{proportion of the offspring produced by sires retained in the second selection} \]

\[ Y_2 = \text{average age of sires saved in the second culling when their subsequent offspring are born} \]

\[ \Delta D_1, M_1, Z_1, \Delta D_2, M_2, \text{and } Z_2 \text{ have corresponding meanings for dams retained in the first and second cullings.} \]

The general principles that govern progress from selection are the same for a whole breed as for a single closed herd. It is impractical to consider here the many forms that herd differences (genetic and environmental) may take, and they are ignored in the formulas for calculating \( \Delta S_1, \Delta S_2, \text{ etc.} \) This procedure favors the progeny test, since the use of progeny averages helps to minimize errors in selection from random environmental variation within a herd but does not lessen those from environmental differences between herds unless a sire has progeny in more than one herd.

**GENETIC SUPERIORITY FROM FIRST CULLING (\( \Delta S_1 \) and \( \Delta D_1 \))**

In estimating the selection differential or average gain in apparent merit of a selected group as compared with the group from which it was chosen (\( i \)), it is assumed that the basis of selection (\( I \)) is normally distributed and that all individuals below a given level are culled. The expected size of the differential or apparent gain in either sex depends on the proportion saved (\( p \)), as illustrated in figure 2. In

![Figure 2](image-url)

**Figure 2.**—A normal distribution showing how a population may be sharply divided at a point (\( k \)) into a selected (\( p \)) and a discarded (1-\( p \)) fraction. The average superiority in apparent merit of the selected fraction is (\( i \)).
livestock breeding, \( p \) (and consequently \( i \)) is largely determined by such factors as rate of reproduction, longevity, and age at puberty, peculiar to each type of livestock. Values of \( i \) in standard deviation units for different values of \( p \) are given for normally distributed populations of infinite size by Pearson (10) and may be calculated from Fisher and Yates (1) for smaller populations (from 2 to 50).

Since the selected group is chosen because of its superiority for some trait \((X)\) or index \((I)\) that is never perfectly correlated with transmitting ability \((G)\), the average genetic superiority expected from the first selection is

\[
\Delta S_1 \text{ or } \Delta D_1 = (\bar{i})_1 b_{g1} \sigma_{I1} = (\bar{i})_1 r_{g1} \sigma_g.
\]

Here \( \bar{i} \) represents the selection differential in standard deviation units, \( b_{g1} \) the regression of transmitting ability on apparent merit, \( r_{g1} \) the corresponding correlation, and \( \sigma_g \) the standard deviation of transmitting abilities. It is convenient to calculate \( r_{g1} \) and \( \sigma_g \) in terms of the hereditary and environmental portions of the observed variance of the population; for example, when the first selection is made on some phenotypic trait \((X)\),

\[
r_{gX} = \sqrt{\frac{G}{E+G}} = \sqrt{G}, \text{ and } \sigma_g = \sigma_X \sqrt{G},
\]

where \( G \) is the heritability or fraction of the observed variance caused by individual differences in transmitting ability \( \left( \frac{\sigma_g^2}{\sigma_X^2} \right) \) and \( E \) is the remaining fraction attributed to environment, dominance, and epistasis or gene interaction \( \left( \frac{\sigma_E^2}{\sigma_X^2} \right) \).

ADDITIONAL GENETIC SUPERIORITY FROM SECOND CULLING (\( \Delta S_2 \) AND \( \Delta D_2 \))

All the culling possible may be done on the basis of the first information available, in which case \( \Delta S_2, N_2, \text{ and } Y_2 \) (or \( \Delta D_2, M_2, \text{ and } Z_2 \)) become zero in formula (1). If the number of animals retained in the first culling permits a second culling after additional information \((O)\), such as the progeny test, becomes available, the maximum additional genetic superiority from the second culling is

\[
\Delta S_2 \text{ or } \Delta D_2 = (\bar{i}_2) R'_{g-1,0} \sigma_g.
\]

Distinction is made between the multiple correlation \( (R'_{g-1,0}) \) and standard deviation of transmitting abilities \( (\sigma_g') \) among animals retained in the first culling, as compared with those in an unselected
group \( (R_{o,t}, \sigma_o) \), because it is mathematically convenient to calculate the former in terms of the latter.\(^5\)

The selection differential for the second culling \( (\bar{t}_2) \) can be calculated from table 20 of Fisher and Yates (1) since it is not affected materially by the slight skewness expected in the distribution of \( R_t \).\(^6\)

**EFFECTIVENESS OF SELECTION FOR IMPORTANT TRAITS OF FARM ANIMALS**

A regular plan of progeny testing may be effective in increasing rate of progress in one kind of animal but not in another even for similar traits, or for one kind of trait but not for another in the same population. The effectiveness depends largely on the age of parents when progeny-test information becomes available, but to some extent also on the rate of reproduction and the relative accuracy of information used for the first culling. Obviously these factors differ for particular kinds of animals and traits.

Several examples that illustrate the influence of these factors on the effectiveness of the progeny test have been chosen. These examples were selected because of their economic importance and because of the extensive breeding research that is being directed toward their improvement. They illustrate the effectiveness of the progeny test when used in conjunction with earlier selection based on pedigree, on individual performances, and on performance of collateral relatives, each of these plans being peculiarly fitted to making early selections for a different kind of trait.

**TRAITS MEASURED IN BOTH SEXES BEFORE BREEDING AGE**

Many important traits, such as growth rate, economy of feed utilization, market conformation, fleece weight, and fleece length, can be measured in both sexes before breeding age. The standard deviation of transmitting abilities among the group saved in the first culling is

\[ \sigma_g = \sigma_o \sqrt{1 - \rho^2} \]

where \( \sigma_g \) is the fraction of the original variance of \( G \) that remains in the selected group. Values of \( \sigma_g \) (hereafter designated as \( \sigma_g^2 \) for sires and \( \sigma_d^2 \) for dams) may be calculated for large populations from the formula

\[ \rho = 1 - \frac{1}{(1 - \rho^2)} \]

suggested by Professor Cochran, where \( \rho \) is the plus or minus deviation from the mean of the unselected population at the point of truncation of the normal curve (fig. 2).

The multiple correlation of \( G \) with \( G \) and \( I_t \) among animals retained in the first culling is

\[ R_{G,GT}^2 = \left( 1 + \frac{\rho^2}{1 - \rho^2} \right) \]

The correlation between \( G \) and \( I_t \) among those selected in the first culling is

\[ r_{G,IT} = \frac{\rho}{\sqrt{1 - \rho^2}} \]

whereas that between \( G \) and \( O \) is

\[ r_{G,O} = \frac{\rho \sqrt{1 - \rho^2}}{\sqrt{1 - \rho^2}} \]

for sires, and

\[ r_{G,D} = \frac{\rho \sqrt{1 - \rho^2}}{\sqrt{1 - \rho^2}} \]

for dams.

\(^4\) The exact selection differential expected in the second culling \( (\bar{t}_2) \) of a population of infinite size was calculated by a method, suggested by Professor Cochran, for varying proportions retained in the first \( (p_1) \) and second \( (p_2) \) culling and for different degrees of correlation between \( G \) and \( I_t \) in the unselected population. Even when \( p_1 \) is as large as 0.8, the exact value of \( \bar{t}_2 \) expected does not differ appreciably, because of skewness, from that expected for a normal distribution unless \( p_1 \) is much larger or smaller than 0.5. For example, when \( p_1 = 0.2 \), \( r_{1,t} = 0.1 \), and \( r_{t,1} = 0.8 \), the exact expectancy for \( \bar{t}_2 \) is only 3 percent higher than for a normal distribution. In the examples that follow, \( p_1 \) is never larger than 0.5 nor smaller than 0.1 and \( r_{1,t} \) does not exceed about 0.5.
measured on both males and females before they reach breeding age. The annual progress expected from selection based on individual performance alone in swine and sheep as compared with that expected from the supplementary use of the progeny test is indicated in the examples that follow.

When first selections are based on individual performance \((X)\) alone, the genetic superiority expected from the first selection is

\[
\Delta S_1 \text{ or } \Delta D_1 = \overline{(\mu)} G \sigma_x. \tag{4}
\]

When second selections are based on the optimum combination of individual performance and progeny test (formula 3), the additional genetic superiority expected is

\[
\Delta S_2 = \overline{(\mu)} G \sigma_x \sqrt{\sigma_u^2 + \frac{nd(1-G)^2}{4(A+nB)+ndG(1-G)-nG^2(1-\sigma_u^2)}} \tag{5}
\]

for sires, and

\[
\Delta D_2 = \overline{(\mu)} G \sigma_x \sqrt{\sigma_u^2 + \frac{n(1-G)^2}{4(A+nB)+nG(1-G)-nG^2(1-\sigma_u^2)}} \tag{6}
\]

for dams, each of which produces one litter of \(n\) progeny. The symbols and their interpretations in terms of the hereditary and environmental fractions of the variance are as follows:

- \(L\) = fraction of total variance due to differences in environment and in gene interaction that are alike for members of the same litter
- \(E\) = fraction that behaves as random environmental variation between litter mates
- \(A\) = fraction due to differences between litter mates = \(E + G/2\)
- \(B\) = fraction due to differences between paternal half-sibs, less \(A = L + G/4\)
- \(C\) = fraction due to differences between nonsibs, less \(A + B = G/4\), so that \(G + L + E = A + B + C = 1\)

In addition,

- \(n\) = number of offspring per litter, and
- \(d\) = number of litters per sire.

Weight at 180 days may be used as an example for swine, in which \(G = 0.30, L = 0.20, E = 0.50, \) and \(\sigma_u = 32\) pounds, in accord with values found by Whatley (14) and Hazel (2). We shall consider a 20-sow herd in which breeding stock are saved from the spring farrow only and \(n = 5\). The age when offspring are born is 1 year for young boars and gilts and 2 years for the tested boars and sows. The selection differentials for formulas (4), (5), and (6) are calculated from table 20 of Fisher and Yates (1). For example, if 3 young sires are saved annually, \(p = 3/50\), so that, for sires, \((\overline{\mu}_1) = 1.91\). When the best 1 of the 3 is kept after testing, \(p = 1/3\) and \((\overline{\mu}_2) = 0.85\). The curves for annual progress in figure 3 were constructed from formula 1. Solid lines show progress expected from the use of 2, 3, and 4 young sires and 1 boar tested the year before, when no tested sows are used \((M_2 = 0)\), but the proportion of the litters by the tested boar \((N_2)\) varies from 0 to 0.8. Broken lines show progress expected as the
proportion of litters farrowed by 2-year-old sows \((M_2)\) varies from 0 to 0.5, when all litters are sired by 2 young boars \((N_2=0)\).

Figure 3, A, (solid lines) shows that \(\Delta G\) is maximum when 2 young sires are used each year on all sows. The use of 3 or 4 young sires decreases progress, as does increasing the proportion of offspring by tested sires. The use of 1 young sire instead of 2 would not increase \(\Delta G\) since all offspring would then be paternal half-sibs, and the reduced genetic variability and heritability would more than cancel the slightly larger selection differential. Even a plan of testing the optimum number of 6 to 8 sires in an auxiliary herd of 20 sows and using the 2 best ones in the closed herd does not increase \(\Delta G\), as shown at the extreme right of figure 3, A. This indicates that the progeny test for sires is not effective for this or similar traits in swine, regardless of herd size.

Figure 3, A, (broken lines), also shows that \(\Delta G\) is about the same when the optimum proportion of the litters (10 to 20 percent) is from...
tested sows as when only gilts are used. As \( M_2 \) is increased, the first selection of gilts becomes more effective, the second selection of sows becomes less effective, and the average age of dams increases. Up to \( M_2 = 0.2 \) the opposing influences nearly cancel, but as \( M_2 \) is increased further, progress declines.

It is apparent from formulas (5) and (6) that progeny testing is more likely to increase progress for traits of lower heritability (\( G \) smaller, \( E \) larger) that are unaffected by litter environment (\( L = 0 \), \( B = G/4 \)). As a population becomes more uniform genetically owing to inbreeding (\( f \)), heritability declines (that is, \( G \approx \frac{G_1 (1 - f)}{1 - G f} \)). For example, as \( f \) rises from 0 to 0.67, the heritability (\( G \)) of growth rate in swine would change roughly from 0.30 to 0.125, \( L \) from 0.20 to 0.25, and \( E \) from 0.50 to 0.625. Figure 3, B, shows that progeny testing of boars or sows does not increase \( \Delta G \) even at this lower level of heritability, although the reduction in \( \Delta G \) from the use of a tested boar is less marked. \( G \) and \( L \) appear to be a little smaller for conformation score at market weight, as shown by Stonaker and Lush \((12)\), than for growth rate of swine, but not enough so to make use of progeny-tested sires advantageous.

The influence that rate of reproduction has on the effectiveness of the progeny test may be illustrated by comparing selection for body weight or fleece length in yearling sheep with that for growth rate in swine. The influence of the time required to obtain progeny tests of sires is shown by comparing selection for yearling traits with that for weaning traits in sheep. Table 1 shows the age distribution, fertility, and average age of dams expected in a flock of 100 ewes if all voluntary culling of females were done before breeding age. In the first selection the best 44 percent of the 50 ewe lambs or yearling ewes and the best 2, 3, or 4 of the 50 ram lambs or yearling rams are chosen. Formulas (4) and (5) may be used in calculating \( \Delta D_1 \), \( \Delta S_1 \), and \( \Delta S_2 \) \((\Delta D_2 = 0, n = 1, \text{ and } A + nB = 1 - G/4)\).

**Table 1.** Age distribution, fertility, and average age of dams at lambing time in a flock of 100 ewes, when all voluntary culling is done before breeding age

<table>
<thead>
<tr>
<th>Age of females (years)</th>
<th>Ewes of each age per 100 breeding ewes</th>
<th>Lambs weaned per ewe</th>
<th>Fraction of all lambs weaned</th>
<th>T for ewes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(1)</td>
<td>(2)</td>
<td>(3)</td>
<td>(4)</td>
</tr>
<tr>
<td>0.</td>
<td>22.0</td>
<td>Number</td>
<td>0.62</td>
<td>0.129</td>
</tr>
<tr>
<td>1.</td>
<td>21.4</td>
<td>Number</td>
<td>0.93</td>
<td>0.194</td>
</tr>
<tr>
<td>2.</td>
<td>20.9</td>
<td></td>
<td>1.22</td>
<td>0.222</td>
</tr>
<tr>
<td>3.</td>
<td>19.7</td>
<td></td>
<td>1.17</td>
<td>0.192</td>
</tr>
<tr>
<td>4.</td>
<td>18.3</td>
<td></td>
<td>1.12</td>
<td>0.153</td>
</tr>
<tr>
<td>5.</td>
<td>16.4</td>
<td></td>
<td>1.10</td>
<td>0.120</td>
</tr>
<tr>
<td>6.</td>
<td>15.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.</td>
<td>14.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>143.4</td>
<td></td>
<td></td>
<td>1.000</td>
</tr>
</tbody>
</table>

1 These data were taken from a report by Terrill \((14)\) on the Rambouillet flock of the United States Sheep Experiment Station and Western Sheep Breeding Laboratory, Dubois, Idaho. They have been adjusted for voluntary culling after breeding age and for a 100-percent lamb crop at weaning age. The figures for ewe lambs and yearling ewes represent those necessary for replacements.

Figure 4, A, shows yearly progress for weanling (solid lines) and for yearling (broken lines) traits when heritability is 0.30 and rams are used first as yearlings. Use of the best ram tested the year before
on the optimum proportion (0.6 to 0.7) of the ewes increases progress by about 4 percent for weanling traits but reduces progress for yearling traits, as compared with the use of only the 2 best yearling rams each year. The difference occurs solely because selection of rams on progeny performance can be made a year earlier for weanling than for yearling traits. As shown at the extreme right of the figure a still greater increase in progress (6 percent) could be obtained for weanling traits by testing the optimum number (7) of yearling rams each year in an auxiliary flock of 100 ewes and using the 2 best ones

![Figure 4](image_url)

**Figure 4.**—Influence of progeny testing of rams on genetic progress from selection for weanling and yearling traits in a closed 100-ewe flock of sheep, when early culling is based on individual performance. *A*, When $G=0.30$, $L=0$; *B*, when $G=0.10$, $L=0$. $s =$ number of sires tested each year.

in the main flock the following year as 2-year-olds. This plan is not effective for yearling traits, however.

When heritability is only 0.10 (fig. 4, *B*) use of the best progeny-tested ram is expected to increase progress about 11 percent for weanling traits and 3 percent for yearling traits. By using the auxiliary flock for testing rams, the increase in progress would be raised to 20 percent for weanling traits and 5 percent for yearling traits.

Progress for weanling traits could be increased still further by testing each of the best ram lambs on a small number of ewes and then using the best tested rams as yearlings instead of as 2-year-olds.
For example, suppose the 4 best ram lambs were tested on 40 ewes and the remaining 60 ewes were mated to the best yearling ram tested the year before. Under this plan, yearly progress expected would be 20 and 28 percent greater, for heritabilities of 0.3 and 0.1, respectively, than if the 2 best untested yearling rams were used on the entire flock, whereas the advantage of testing yearling rams and using the best tested 2-year-old is only 4 and 11 percent, respectively. The increase in progress from testing rams in the auxiliary flock of 100 ewes is also greater if the tested rams can be used in the main flock as yearlings instead of as 2-year-olds (22 and 37 percent, respectively, for heritabilities of 0.3 and 0.1, instead of 6 and 20 percent). These maximum estimates of the gain in rate of improvement from using progeny-tested rams are far below the 500 percent gain claimed by McMahon (9) for heritability at 0.10. The discrepancy appears to be due largely to McMahon's assumptions that (1) the average of 7 progeny is perfectly correlated with the sire's genotype and (2) the interval between generations would not be lengthened by using tested rams. Actually, the correlation of a ram's genotype with the average of 7 progeny would be little larger ($r_{ga} = 0.39$) than with the ram's own phenotype ($r_{gx} = \sqrt{0.10} = 0.32$), in an unselected population and for heritability at 0.10. For weanling traits, the generation interval could actually be shortened a little, compared with the use of untested yearling rams, by testing ram lambs on part of the flock and using tested rams as yearlings on the rest of the ewes. However, progeny tests for yearling traits on rams used as lambs or yearlings would be obtained only in time for use of selected tested rams as 2- or 3-year-olds, and use of tested rams would lengthen the generation interval by 6 months or 1 year compared with the use of untested yearling rams.

**TRAITS MEASURED ONLY AFTER SLAUGHTER**

Information on collateral relatives may not be of sufficient importance for traits measured in both sexes before breeding age to be considered in making selections. For traits measurable only in the carcass, there may be no other basis for making early selections. In a closed herd of swine, for example, several pigs from each litter may be slaughtered at market weight, the information being used in selecting collateral relatives and for progeny-testing the previous group of young sires.

The genetic superiority for a carcass trait ($X$) of boars or gilts selected in the first culling based on the average of $n$ litter mates is

\[
\Delta S_1 = \bar{t}_1 G \sigma_x \sqrt{\frac{n}{A+n(B+C)}}. \tag{7}
\]

The additional genetic superiority from the second culling based on the optimum combination of the average of $nd$ progeny and of $n$ litter mates is

\[
\Delta S_2 = \bar{t}_2 \frac{G}{2} \sigma_x \sqrt{n \left[ \frac{(A+nB)^2}{A+n(B+C)} - n^2 \sigma_x^2 (d+1-\sigma_e^2) \right]} \tag{8}
\]
for sires, and

$$\Delta D_2 = \frac{\bar{G}}{2} \sigma x \sqrt{\frac{n}{A+n(B+C)}} \left[ \frac{(A+nB)^2}{[A+n(B+C)]^2 - nC^2(2-\sigma_y^2)} \right]$$

for dams having only one litter. The symbols used are those defined for formulas (4) to (6).

The curves in figure 5 are for a closed 20-sow herd in which carcass traits are observed on 2 pigs from each litter and when the s young boars and the gilts used for breeding each year are chosen from 40 gilts in 20 litters and 10 boars in 10 litters. Use of the best sire tested the preceding year reduces progress expected when heritability is 0.50 (fig. 5, A), although progress is increased about 10 percent if optimum proportion of the litters (about 0.2) is from the best sows tested the year before. When heritability is as low as 0.10 (fig. 5, B), the progeny test is slightly effective. As shown at the extreme right of figure 5, progress is not increased by testing the optimum number (7) of boars in an auxiliary herd of 20 sows and using the best 2 in the main herd the next year.

Thus it seems unlikely that progeny testing can increase progress for carcass traits in swine appreciably if earlier culling of breeding animals can be based on the average performance of several litter
mates. However, progeny tests are much more likely to be helpful in selecting for such traits in beef cattle or sheep, where the reproductive rate is lower and earlier culling must be based on the performance of half-sibs rather than full sibs.

REPEATABLER TRAITS EXPRESSED ONLY IN THE FEMALE

Progeny testing of sires might be presumed to have special usefulness in selecting for such traits as butterfat production in dairy cattle or prolificacy in swine, since early culling must be based largely on pedigree. Because progeny tests have received so much attention both in the literature and in the practice of dairy-cattle improvement, butterfat production has been used in the example that follows.

The genetic superiority for butterfat production \((X)\) expected for bull or heifer calves selected in a first culling based on an average of \(k''\) records for each of the dams is

\[
\Delta S_i = \left( \frac{G}{2} \right) \sqrt{\frac{k''}{E_r + k''(E_p + G)}},
\]

where the intraherd variance in butterfat production \(\sigma_x^2\) is subdivided into the following fractions:

\(G\) = heritability or fraction due to differences in transmitting ability

\(E_p\) = fraction due to permanent differences in environment, to deviations from transmitting ability due to dominance and epistasis, and

\(E_r\) = fraction due to random variation in environment between different records of the same cow, after adjustment for age.

The additional genetic superiority expected for sires selected in a second culling based on the best combination \((I_2)\) of the average production for \(d\) daughters with \(k\) records each and the average of \(k''\) records of each sire’s dam is (from formula 3)

\[
\Delta D_2 = \frac{\left( \frac{G}{2} \right) \sigma_x}{2 \sqrt{E_r + k''(E_p + G)}}.
\]

The additional genetic superiority expected for dams selected in a second culling based on the best combination of each cow’s own average for \(k'\) records and her dam’s average for \(k''\) records is

\[
\Delta D_2 = \frac{\left( \frac{G}{2} \right) \sigma_x}{2 \sqrt{E_r + k''(E_p + G)}}.
\]

The results to be expected from progeny testing of dairy sires are shown in figure 6 for a closed herd of 120 cows. Heritability \((G)\) is 0.25 in figure 6, \(A\), and 0.10 in \(B\), but repeatability \((G+E_p)\) is 0.35 in both. These are roughly the upper and lower limits of herita-
bility indicated in such studies as those of Lush, Norton, and Arnold (7) and Lush and Straus (8). In this example, one-fourth of the cows are replaced each year; only calves from three-fourths of the cows that have completed one or more records are considered in selecting breeding animals; and 90 percent of the cows raise calves each year. Three-fourths of the heifer calves (30/40) are saved in the first culling and kept for two lactations, after which one-half (15/30) are retained in the second culling for an average of 4 more lactations. Thus the average age of dams when the calves from which breeding stock are chosen (second record and later) are born is about 4 years; that is, \[ 3 \text{ years} \div 3 = 1 \text{ (5.5 years)}. \] The average number of records per dam is \( k'' = 2 \). Also, young sires selected for progeny testing and used for 1 year when from 15 to 27 months of age are about 2\frac{1}{2} \text{ years old} when their calves are born (that is, \( Y = 2\frac{1}{2} \text{ years} \)). When the 1 best sire tested over each 2-year period (on the basis of \( d \) daughters with \( k = 1 \text{ record each} \)) is used again on part of the herd for a 2-year period, his average age when his second group of calves is born will be about 8 years (that is, \( Y = 8 \text{ years} \)). Under these conditions, the annual progress expected is

\[
\Delta G_t = \frac{N_1(\Delta S_1) + N_2(\Delta S_1 + \Delta S_2) + \%(\Delta D_1 + \Delta D_2)}{2.5N_1 + 8N_2 + 4\%}.
\]

Figure 6 shows that the progeny test is not effective under the conditions stated, \( \Delta G_t \) decreasing as \( N_2 \) increases.

The total annual progress (\( \Delta G_t \)) is subdivided in figure 6 into that from the two successive cullings among females (\( \Delta G_d \)) and that from the two cullings among males (\( \Delta G_s \)). As Seath (11) has shown, much of the culling among females is for disease, breeding failure, and similar causes, so that \( \Delta G_d \) for butterfat production actually may be considerably less than indicated in figure 6. This would make the curves for \( \Delta G_t \) more nearly like those for \( \Delta G_s \), which show the progeny test in a more favorable light. If no progress is made from selection of dams (\( \Delta G_d = 0 \)), progress from sire selection (\( \Delta G_s \)) is optimum when one-third to one-half of the cows are bred to the best 1 of 4 sires tested during the 2 preceding years, and \( \Delta G_s \) is increased about twice as much (10 percent as compared with 5 percent) by progeny testing when heritability is 0.10 as when heritability is 0.25.

Use of progeny-tested dairy sires would be a little more likely to increase the rate of improvement if, instead of the average production of the daughters alone being used, that of the dams to which each sire was mated were also considered properly. This procedure, according to Lush (6), would make progeny tests in a population of many herds about 1.12 to 1.20 times as accurate as the use of the average production of the daughters alone. The exact amount depends largely on the correlation between the average production of the sire's daughters and that of their dams, and would, therefore, be less for comparisons between sires tested in the same herd and during the same years. In the above example (when selection of dams is presumed ineffective), increasing the accuracy of progeny tests 1.10 times would change the percentage increase in yearly improvement resulting from optimum use of tested sires only, from 10 to 13 if heritability is 0.10 and from 5 to 8 if heritability is 0.25.
DISCUSSION

The foregoing examples indicate that the possibilities of increasing progress by a regular plan for use of progeny-tested sires are limited to certain kinds of livestock and to certain traits. The reasons for this limitation may be illustrated by comparing the effectiveness of
progeny testing in the different examples. First, the less the interval between generations is increased by progeny testing the more likely it is that progeny testing will increase progress. This is shown by contrasting the results of selecting for weanling and yearling traits in sheep (fig. 4). The only difference in these examples is that 1 year is required to obtain progeny-test information on weanling traits, whereas 2 years are required for yearling traits. Second, when the rate of reproduction is low, progeny testing of sires is more likely to increase progress. The resulting increase in genetic superiority of parents ($\Delta G$) tends to be larger, relative to that in the age of parents ($T$), when there is less opportunity for early culling, particularly among females. This is the reason that progeny testing affects progress more favorably for yearling traits in sheep (fig. 4) than for growth rate in swine (fig. 3), and when little voluntary culling of females is possible for butterfat production in dairy cattle ($\Delta G$, in fig. 6). Third, if the basis for making first selections is relatively inaccurate, the progeny test is more likely to be effective, because there is more environmental variation to be discounted by the progeny test and more of the genetic variation remains among animals tested. This is illustrated by the contrast in the effectiveness of the progeny test for high and low heritability (figs. 3, 4, 5, and 6).

Thus a combination of circumstances, largely beyond the breeder's control, operates to make the use of a regular plan of progeny testing a wise or unwise procedure. In many cases when the progeny test is most easily applied it may actually reduce genetic progress (fig. 3). Even when the circumstances indicate the use of progeny-tested sires, there is danger that its full effectiveness will not be realized in practice because of unwise judgment. Too many or too few young sires may be tested on too many or too few females, so that the optimum use of young and tested sires is not attained (fig. 4). Although little attention has been given to this point, it becomes important once a breeder decides to use a regular plan of progeny testing.

The progeny test is not likely to be more effective in increasing genetic progress in actual practice than under the conditions assumed in the foregoing examples. Where assumptions had to be made, these generally favored the progeny test. For example, the average of a sire's offspring was assumed to be unbiased because of special treatment or selection among the offspring before the trait ($X$) was measured. Although the sharp truncation assumed here is not likely to exist in actual practice, particularly for any single trait, this seemingly overestimates the selection differential for all age groups in both sexes. This favors the older animals, since more culling for age, sterility, disease, and other factors and more deaths would occur among them.

It was necessary to assume that the genetic gain from the first and the second selections ($\Delta S_1$ and $\Delta S_2$ or $\Delta D_1$ and $\Delta D_2$) was constant from year to year. Of course, this would not be exactly true, particularly for small herds. Nevertheless, the estimates of $\Delta G$ in the foregoing examples represent the average expectancy for any of the plans for regular use of progeny-tested sires. The effectiveness of progeny testing would be somewhat greater than indicated in these examples if a tested sire were used only when one of exceptional merit was found, or if the proportion of the herd mated to the tested sire were varied according to his apparent superiority. Although there are
some notable cases in which the progeny test has identified animals of exceptional transmitting ability, these cases are rare in breed histories and offer uncertain possibilities to the individual breeder who can test only a limited number of sires. Breeders who regularly use the best young sires extensively would be better able to recognize and make use of the occasional outstanding sire, if still available, than breeders who regularly use a tested sire on most of the herd and use young sires sparingly.

For simplicity, selection for one trait at a time was considered in the examples. Methods have been developed by Hazel (2) for expressing net merit as a linear function of several traits, including the performance of relatives. The relative effectiveness of the progeny test in selecting for an index based on several traits would be much the same as that for a single trait. In fact, the formulas developed herein for individual traits could be applied directly to more complicated cases by considering the index as a single trait.

The effect of progeny testing on the genetic progress in an entire breed is much the same as in a closed herd. A breed is just a much larger closed herd, in which another source of variation, herd differences, must be considered and in which inbreeding may be a negligible factor. Thus the same general conclusions for selection within closed herds apply for the much larger closed population of an entire breed. The regular use of progeny tests does not increase, and may decrease, the rate of progress unless the progeny-test information can be obtained early, the reproductive rate is low, and there is little or no basis for earlier culling.

These conclusions do not conflict in any way with the fact that unbiased progeny-test information always increases the accuracy of selection for traits that are influenced much by dominance, epistasis, or environmental variations. They simply mean that in the time required to carry out the progeny test the genetic progress from selection based on pedigree, individual merit, or family averages may be more than that obtained from selection on the progeny test. For the improvement of most traits, in most kinds of livestock, these conclusions point unmistakably toward the fuller use of pedigree, individual merit, and family averages for early culling in order to keep the interval between generations short and progress maximum.

The technique of artificial insemination may increase the advantage of using selected progeny-tested sires if the population is sufficiently large and if the reproductive rate of males is increased markedly thereby, as in sheep and cattle. If fewer sires are needed, more progress is expected from the more intense selection of young sires. However, mating each young sire to larger numbers of females also is likely to increase the accuracy of selecting between tested sires more than enough to offset the increased intensity selection of young sires, particularly for traits low in heritability.

In the literature, progeny testing does not always refer to use of progeny-tested individuals. The progeny-test breeding so successfully practiced on laboratory animals, poultry, and plants is often based on selection between and within the progenies themselves rather than between parents on the basis of the progeny test, and consequently does not increase the interval between generations. Actually, this is selection based on a combination of individual performance and family average. It differs from the methods indicated for farm live-
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stock only in the greater emphasis on selection between families or progenies which a higher reproductive rate permits.

SUMMARY AND CONCLUSIONS

Annual improvement from selection in a closed herd or breed is the ratio of the average genetic superiority of parents (compared with the unselected group from which they were chosen) to the average age of parents when offspring are born.

Examples of progress expected from selection based on pedigree, individual performance, or averages for collateral relatives, with and without the supplementary use of the progeny test, have been given for representative economic traits of farm animals.

A regular plan of progeny testing is unlikely to increase, and may reduce, progress unless (1) the progeny-test information becomes available early in the tested animal's lifetime, (2) the reproductive rate is low, and (3) the basis for making early selections is relatively inaccurate. These factors are largely beyond the breeder's control, being relatively unchangeable for a particular kind of animal and trait.

Opportunity for improvement from selection is nearly maximum for most traits when (1) culling is based on individual performance, family average, and pedigree and (2) the interval between generations is kept short. Possible exceptions are weanling traits in sheep and carcass traits in sheep and beef cattle.

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