1960

Optimum length of the feeding period for selection of beef cattle

Louis Andre Swiger
Iowa State University

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OPTIMUM LENGTH OF THE FEEDING PERIOD
FOR SELECTION OF BEEF CATTLE

by

Louis Andre Swiger

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

Major Subject: Animal Breeding

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa
1960
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additional information that was not contained in the early part of the test. This might occur if the genes which affect gains in the early part of the test persist in their effects, or if performance in gain in the later part of the feeding period is influenced very little by the genes an animal has. Genetic and phenotypic parameters for gain in weight among five 28-day feeding periods were of primary interest in this study. The relations among those parameters and those involving birth weight and weaning weight were also of interest.
REVIEW OF LITERATURE

Only a few studies which were pertinent to the problem of measuring genetic ability to gain weight from phenotypic gain during different periods of life were found in the literature. These were included in this section. Environmental effects, heritabilities and genetic correlations from the literature appear in the discussion where they are compared to the results of this study.

Hazel et al. (1943) studied the genetic and environmental relations among gain in three successive 56-day periods in swine. The first period began at birth. Phenotypic, environmental and genetic variances and covariances were computed by a paternal half-sib analysis. Of the three periods the second was the most efficient measure of hereditary growth rate over the 168 days. Hereditary growth rate was defined as 

\[ G_t = \sum G_i \]

where \( G_i \) is the sum of the average effects of the genes for gain in the \( i \)th period, and \( G_t \) is a similar value measured over the total of all periods. The first period, pre-weaning growth, was the least efficient. Since the heritabilities were small (.15, .28, .17) and the genetic correlations were large (.70 and .71 between adjacent periods and .45 between the other two), they concluded that heredity exerted a less important but more constant influence on growth over the entire period than did environment.
Using the methods given by Hazel et al. (1943), Knapp and Clark (1947) studied the relations between growth of beef cattle in three 84-day periods of a feeding test. Their heritabilities increased for successive periods (.10, .54, .84). Genetic correlations between adjacent periods were larger (.82, .70) than between the two periods separated by 84 days (.45). Environmental correlations were small or negative (.11, -32, .13) and phenotypic correlations were intermediate (.26, .39, .18). The correlations between hereditary growth rate ($G_t$) and phenotypic gain in each period were .23, .69 and .85. The correlation between $G_t$ and total gain was .85 and the multiple correlation between $G_t$ and gain in each period was .94. The authors concluded that for the length of the feeding period used in this study a progressively better measure of genetic growth was obtained as the feeding period progressed. They suggested the feeding period should not be less than 252 days.

Urick et al. (1957) conducted a similar study with cattle using an 140-day feeding test the first winter, summer gains on pasture and a 112- to 135-day feeding test the second winter as three measures of gaining ability. Heritabilities were .34, .43 and .09, respectively. Genetic correlations were .45 and .87 between adjacent periods and .99 between the two winter feedlot periods. Environmental correlations were -.14 and -.21 between adjacent periods and .19 between winter
gains. The corresponding phenotypic correlations were .07, .02 and .32. They concluded that gains during the three growth periods seemed to be influenced by the same block of genes and that genes responsible for growth during the two winter periods and for the summer and second winter period were very similar.
SOURCE OF DATA

The data were taken from the records of a herd of pure-bred Hereford cattle, owned by Charles E. Haigler, and located near Washington Court House in southern Ohio. Mr. Haigler uses the data for selecting replacement animals in his own herd. The data are available to potential buyers of breeding stock offered for sale.

The cows are bred to calve starting the first week in April and most of the calves are born during April and May. The calves are weaned on the same day each year. The weaning date varied from late November to early January for the years included in this study. A few late summer calves are born each year. These calves are not started on the feeding test and were omitted from this study.

At weaning time the calves are started immediately on a feeding test of 140 days. No selection is practiced prior to the termination of the feeding period.

During the post-weaning feeding period the calves are separated by sex, the bulls being fed in one pen and the heifers in an adjoining pen. The pens are covered by a roof, but three sides remain open, a barn forming a solid side to the west. Concentrates are fed free choice in round self-feeders within the pens. Hay is fed in racks in the pens and grass silage is fed in bunks along the outside of the pens. The calves are fed as much hay as they will "clean up" each
day and are given a small amount of grass silage.

The concentrates fed to the calves are coarsely ground corn and cob meal containing eight to nine percent soybean oil meal. The hay and grass silage are either mixed alfalfa and bromegrass or alfalfa and timothy. Pastures are either permanent bluegrass or rotation pastures of alfalfa and bromegrass or alfalfa and timothy. A mineral mixture of limestone, bone meal and salt is fed free choice in the pens and pastures.

The cow herd is turned onto stalk fields after the corn is picked. Following this they are wintered on hay and grass silage. Females are fed small amounts of corn and cob meal during the winter until after their second calf is born.

During the calving season the pastures are checked daily by a man driving a pick-up truck. New calves are weighed on a portable scale carried in the truck, tattooed and identified with their dams. All calves are weighed at weaning and at the end of each successive 28 days for 140 days following weaning.

Since the birth weights were missing for 39 calves, weaning weight was used in this study instead of gain from birth to weaning. Gain for each 28-day period during the feeding test was computed. In 1952 weaning weights were not taken, therefore weaning weight and gain in the first 28-day period were inseparable and were discarded. That is, only birth weight and gain in the last four feeding periods were included
in the analysis for the 1952 calves.

In addition to birth weight, weaning weight and gain in each of five 28-day periods following weaning, the following information was available for each calf. The age of the calf at weaning (thus the age of the calf at the beginning of the test) was computed for each calf since the weaning date for each year and the birth date for each calf were known. The age of the dam of each calf was available. Year of birth, sex, sire, and dam of each calf were also recorded.

Table 1 shows the distribution by year and sex of the 832 calves used in this study. Birth weights were taken on

<table>
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<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulls</td>
<td>38</td>
<td>41</td>
<td>42</td>
<td>43</td>
<td>53</td>
<td>61</td>
<td>67</td>
<td>43</td>
<td>42</td>
</tr>
<tr>
<td>Heifers</td>
<td>33</td>
<td>41</td>
<td>42</td>
<td>36</td>
<td>56</td>
<td>55</td>
<td>48</td>
<td>48</td>
<td>43</td>
</tr>
</tbody>
</table>

793 calves. Weaning weight and gain in the first period were available for only 748 of the calves since the 84 calves born in 1952 were not weighed at weaning. A calf was omitted from the study if any trait was missing except birth weight in any year, or weaning weight and first period gain in 1952. Progeny from 23 sires were included in this study.
ANALYSIS OF DATA AND RESULTS

Environmental Analysis

Data analyzed by the animal breeder are often not from an experiment designed specifically to answer his particular question. In fact, the data often come to him long after they have been collected. Often they are not from a designed experiment at all. This requires statistical control of some important sources of variation which might otherwise have been controlled experimentally. In data on large animals the additional problem of unequal subclass numbers is almost always present even in a carefully designed experiment.

If some sources of variation are fixed and others are random, the problems become even more perplexing. Whether a source of variation is fixed or random is not always apparent. The two points which deserve special consideration here are the manner in which the levels of the questionable variable arose in the data and the kind of population to which the results of the analysis are to be extended. If the levels of a factor were not themselves chosen but are whatever came in a random sample from some population, then this factor is a random one and the results may be extended to a similar population. However, if the levels are particular levels which were chosen because they are of interest in themselves (perhaps the only levels) the factor is fixed and we may make
Inferences only about these levels.

In animal breeding problems the situation is often not clear. Given a set of data such as in this thesis where the sires, for example, are the particular ones used on the farm one might argue that sires are fixed. However, it seems reasonable that the sires are a representative sample of the population of sires which could have been used and may be considered random. In fact, unless this assumption is made the analysis is worth while only if one desires to make inferences about these particular sires.

Sex, age of dam and age of calf might logically be considered as fixed variables in these data. The argument that sires are random seems also to apply to years. Since the effects of the environmental sources of variation were removed from the data by fitting constants with a least squares analysis and correcting the data, whether they are fixed or random was of no consequence. However, sires must be considered random in order to compute the variance component for sires and estimate the genic variance in the population.

The combination of fixed and random variables and unequal subclass numbers presented certain problems in the analysis of these data. Ordinary analysis of variance techniques could not be used to compute variance components and make tests of significance. Least squares analysis as described by Kempthorne (1952) and Henderson (1953) was used.
Table 2 contains the unadjusted mean and standard deviation of each of the seven traits. Since information was available on several sources of variation which are known to affect growth in beef animals, the data could be corrected for these variables before proceeding with the genetic analysis. This is Method 2 of Henderson (1953).

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. of animals</th>
<th>Mean</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth weight</td>
<td>793</td>
<td>72.5</td>
<td>10.0</td>
</tr>
<tr>
<td>Weaning weight</td>
<td>748</td>
<td>431.2</td>
<td>85.6</td>
</tr>
<tr>
<td>First period gain</td>
<td>748</td>
<td>50.2</td>
<td>22.7</td>
</tr>
<tr>
<td>Second period gain</td>
<td>832</td>
<td>50.2</td>
<td>18.4</td>
</tr>
<tr>
<td>Third period gain</td>
<td>832</td>
<td>57.8</td>
<td>19.5</td>
</tr>
<tr>
<td>Fourth period gain</td>
<td>832</td>
<td>54.4</td>
<td>20.4</td>
</tr>
<tr>
<td>Fifth period gain</td>
<td>832</td>
<td>55.1</td>
<td>19.4</td>
</tr>
</tbody>
</table>

Birth weight was corrected for year, sex, and age of dam. Weaning weight and post-weaning gains were corrected for year, sex, age of dam and age of calf at weaning. Yearly differences in rainfall, temperature, herd health, management etc. would be expected to affect these traits by affecting the calf either directly or through its dam. On the average
females have lower birth weights and weaning weights than males and gain less in the feedlot. Age of dam influences birth weight and weaning weight because cows of different ages provide better or worse intra-uterine and pre-weaning environments. Age of dam would influence gain on feed to the extent pre-test environment affects this gain. The age of calf obviously will influence weaning weight and could affect post-weaning gains if the growth curve was not linear during the feeding period.

Least squares analysis requires formulating an additive model which may be written as

$$ y_1 = \sum_{j=1}^{p} x_{1j} b_j + e_1. $$

The $y_1$ is the dependent variable, the $x_{1j}$'s are the independent variables and the $b_j$'s are partial regression coefficients. The e's are random errors assumed to have expectation zero, be uncorrelated, and have a common variance. If the e's are also distributed normally, tests of significance and confidence intervals may be made on the $\widehat{b}$'s ( $\widehat{b}$ denotes estimate). The mechanics of estimating the $b$'s and the characteristics of the estimates have been described by Kempthorne (1952).

The sums of squares removed from the total sum of squares by fitting the model is called the reduction due to fitting the parameters $R(b_1 \ldots b_p)$. To test how well a simpler
model fits the data, compared to the original model, one fits the reduced model

\[ y_i = \sum_{j=1}^{q} x_{ij} b_j + e_i , \quad q < p \]

and computes \( R(b_1 \ldots b_q) \). The difference between the two reductions is the additional sum of squares attributed to \( b_{q+1} \ldots b_p \). Then

\[
\frac{R(b_1 \ldots b_p) - R(b_1 \ldots b_q)}{p - q} \text{ (residual mean square of the full model)}
\]

is distributed as \( \chi^2 \) and this provides a test of how well the reduced model fits the data as compared with the full model.

Before proceeding with the analysis, the assumption of additivity of the main effects was examined. The interactions could have been tested by the general procedure of testing the difference between the reduction computed from a model containing all sources of variation and the reduction of one omitting the particular interaction being tested. To do this repeatedly for each interaction would have been unfeasible computationally since this would have required solving many large sets of simultaneous equations.

Von Krosigk (1959) computed the variance components for each main effect and several two-factor interactions, considering all sources of variation random and equating the sums of squares to their expectations. He then took each variance component as a fraction of the sum of all variance components as a measure of their importance. He arbitrarily decided to
consider further only sources of variation accounting for more than 2.5 percent of the total variation. He pointed out that this yields biased estimates if some factors are fixed. However, this seems to be the only practical way to look at all the sources of variation, including the interactions, simultaneously.

The effect of age of calf on weaning weight has been found in other studies to be nearly linear. The age at weaning varied from 124 to 286 days in this study. The calves were grouped by age at weaning, ignoring year, sex and age of dam, and the mean weaning weight was computed for each group. Figure 1 shows the mean weaning weight plotted against the mean age for each group. A slight departure from linearity exists for both very young and very old calves. This was not considered serious enough to warrant fitting a curve of higher degree for the effect of age of calf on weaning weight.

Figure 2, constructed like Figure 1, shows the effect of age of calf at weaning on gain in the first post-weaning period. The effect appears to be strongly curvilinear. The linear regression computed from the data was negative (Table 5). However, the regression between years was negative and the pooled regression within years was positive. Figure 3 shows the means for each age of calf class after the data were corrected for the effects of year, sex and age of dam, using the constants obtained from the least squares analysis.
Figure 1. Mean weaning weight for each age of calf group
Figure 2. Mean first period gain for each age of calf group
Figure 3. Mean first period gain for each age of calf group corrected for year, sex and age of dam
Figure 3 indicates that the effect of age of calf on gain in the first period is nearly linear. The effect decreases slightly for older calves. The regression of gain on age of calf decreased for each succeeding 28-day period (Table 6). It seems unnecessary to present graphs similar to Figure 3 for the other periods. The effect of age of calf on weaning weight and gain in each period was treated as linear in this analysis.

The effect of age of dam on birth weight, weaning weight and post-weaning gains was strongly curvilinear. Koch's (1953) data were an excellent example of this for weaning weight. Blackwell and Henderson (1955) fitted a quadratic regression for the age of dam effect on weaning weight of sheep.

Other workers have found lighter birth weights for young cows but no decrease with the older ages as was apparent in the present data. However, the decline in this study was for cows from 11 to 17 years of age. The other studies did not contain such old cows.

Treating age of calf and age of dam as continuous variables provided a method for testing all the two-factor interactions except the sex x year interaction. The three-factor interaction of year x sex x age of dam for birth weight, the four three-factor interactions and the one four-factor interaction for weaning weight and post-weaning gains were ignored.
The higher order interactions seemed unlikely to be important, especially if the two-factor interactions were not.

The interactions were first examined by graphing them. For example, Figure 4 shows the yearly average for each sex for birth weight. If the sex difference were equal each year there would be no interaction. That is, the lines representing the two sexes would be parallel.

The graphs could be misleading if other sources of variation were not balanced over the subgroups of the two variables being studied. For example, in Figure 4 the females in 1952 may have been born to younger dams, on the average, than the males. Also it is difficult to decide how different from parallel the lines should be before an interaction is important, since this depends on the size of the error mean square.

Fortunately the year x sex interaction appeared much less important than the other two-factor interactions for each of the seven traits. This interaction was slightly more important for gain in the post-weaning periods than for birth weight and weaning weight. This would be expected since the sex difference also contained the pen difference. Disease, parasites, etc. confined to one pen could vary from year to year. As most of the other interactions were not significant, the year x sex interaction was not considered further.

Since age of dam and age of calf could be treated as continuous variables, tests of significance could be made
Figure 4. Mean birth weight of bulls and heifers for each year
about the remaining five two-factor interactions. These interactions may or may not have been important sources of variation for the traits studied. It was desirable to determine whether an interaction should be considered in explaining the data. Very little information was available from other studies about the interactions of environmental variables in beef cattle data. If an interaction was not judged significant this does not imply it was zero. The computed subclass means for any two-factor interaction, after being corrected for the other important sources of variation, were the best estimates of the true subclass means whether or not the interaction was significant. The question asked by the test of significance was whether the apparent contribution of a particular interaction to the total sum of squares was larger than could reasonably be supposed to be only a sampling variation. If fitting the main effects would explain most of the variation in the subclass means the small additional reduction in the variance gained by fitting the interaction would not be worth the effort of doing so.

For each test, all other sources of variation were ignored and any real effects they had went into the residual sum of squares (as far as the ignored variables were uncorrelated with the variables being tested). This would inflate the residual mean square and make the $F$ ratio smaller than it really should be. Also the number of degrees of freedom for
the residual mean square was slightly higher than it would have been if all the recognized sources of variation were considered simultaneously. With several hundred degrees of freedom available for estimating the residual mean square, this discrepancy was of minor importance.

The general procedure in testing the interactions was to investigate whether a single regression with the independent variable treated as a continuous variable described the data about as well as a separate regression for each level of the discrete variable. For the interaction between age of calf and age of dam, age of dam was treated as the discrete variable.

As an illustration of the general procedure, an example using year and age of dam follows. The full model allowing a regression for each year was

\[ y_{ij} = b_{0i} + b_{1i} x_{1j} + b_{2i} x_{1j}^2 + e_{ij} \]

where \( y \) is the trait for the \( j^{th} \) calf in the \( i^{th} \) year and \( x \) is the age of dam for that calf. The \( b \)'s are zero unless the \( i \) subscript is the same as that of the calf.

The reduced model allows for only one regression representing all years. Since yearly means of the \( y \)'s and \( x \)'s were usually different, an intercept was fitted for each year. Otherwise, even if the curves were identical in shape for each year, the difference between the two models could be
significant if the yearly intercepts varied much. The reduced model was

\[ y_{ij} = b_{0i} + b_{1}x_{ij} + b_{2}x_{ij}^2 + e_{ij} \]

A reduction due to each model was computed and a test of significance was made. Table 3 shows a sample analysis of variance.

Table 3. Sample analysis of variance for testing the interactions

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>R(b_{0i} ... b_{2i})</td>
<td>p</td>
<td></td>
</tr>
<tr>
<td>R(b_{0i} ... b_{2})</td>
<td>q</td>
<td></td>
</tr>
<tr>
<td>difference</td>
<td>p - q</td>
<td>A</td>
</tr>
<tr>
<td>residual</td>
<td>n - p</td>
<td>B</td>
</tr>
</tbody>
</table>

\[ F_{p-q, n-p} = A / B \]

Table 4 shows the results of testing the interactions for significance. The interactions between age of calf and year, and between age of calf and age of dam, were not significant for any trait. The age of calf x sex interaction was significant for weaning weight. This means that bulls and heifers grow at different rates during the age span
Table 4. Results of tests of significance of the two-factor interactions between the environmental effects

<table>
<thead>
<tr>
<th>Interaction</th>
<th>Birth weight</th>
<th>Weaning weight</th>
<th>First period gain</th>
<th>Second period gain</th>
<th>Third period gain</th>
<th>Fourth period gain</th>
<th>Fifth period gain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age of calf x year</td>
<td>NS&lt;sup&gt;a&lt;/sup&gt;</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Age of calf x sex</td>
<td>NS&lt;sup&gt;b&lt;/sup&gt;</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>Age of calf x age of dam</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Age of dam x year</td>
<td>NS</td>
<td>**</td>
<td>*&lt;sup&gt;c&lt;/sup&gt;</td>
<td>NS</td>
<td>**</td>
<td>NS</td>
<td>**</td>
</tr>
<tr>
<td>Age of dam x sex</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>*</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

<sup>a</sup>NS - P > .05.
<sup>b</sup>** - P < .01.
<sup>c</sup>* - .05 > P > .01.
included in these data. Koch et al. (1959) found a difference of 0.11 pounds between the average daily gain of bulls and heifers from birth to weaning. This interaction was also significant for the last gain period. Table 5, which contains the regression coefficients from this analysis, shows a tendency for the age of calf effect to be larger for males throughout the feeding test. The interaction of age of dam and sex was significant only for the third gain period.

Table 5. Regression coefficients of each trait on age of calf in days obtained from testing the sex x age of calf interaction

<table>
<thead>
<tr>
<th></th>
<th>Weaning weight</th>
<th>First period gain</th>
<th>Second period gain</th>
<th>Third period gain</th>
<th>Fourth period gain</th>
<th>Fifth period gain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulls</td>
<td>1.80</td>
<td>-0.14</td>
<td>0.02</td>
<td>0.13</td>
<td>0.23</td>
<td>0.25</td>
</tr>
<tr>
<td>Heifers</td>
<td>1.21</td>
<td>0.04</td>
<td>0.01</td>
<td>0.15</td>
<td>0.07</td>
<td>0.05</td>
</tr>
<tr>
<td>Bulls and heifers</td>
<td>1.51</td>
<td>-0.09</td>
<td>0.01</td>
<td>0.14</td>
<td>0.15</td>
<td>0.13</td>
</tr>
</tbody>
</table>

The age of dam x year interaction was significant for weaning weight and for the first, third, and last gain periods. Several things could have caused the age of dam x year interaction to be large. First, a real interaction could exist. This might be true if the yearly differences in pasture conditions influenced the age of dam effects on
weaning weight. For example, two-year-old cows generally give less milk than three-year-old cows, but in years of abundant pasture the difference between two- and three-year-old cows might consistently be larger or smaller than years when pasture conditions are poor. Second, the year a cow is born determines her age for each subsequent year. Thus a group of cows born in 1948 would be two years old in 1950, three years old in 1951 etc. If, for some trait, a birth-year group of cows was much higher or lower, on the average, than the rest of the herd, the fact that they were a different age in each succeeding year could cause a large sum of squares for the interaction between year and age of dam for this trait. Third, if age of calf, sex, sires, or any other important source of variation were confounded to some extent with age of dam x year subclasses the interaction could appear large. Fourth, in the first six years of the study most cows calved at two years of age. In the last three years the cows had their first calves at three years of age. Therefore the three-year-old class contained both first and second calf heifers, this being confounded with years.

The interaction between age of dam and years was tested again in an analysis which included sex and age of calf. Sires could not be included since this would have made too many equations.

Figures 5 and 6 show the means for birth weight and
Figure 5. Mean birth weight of each age of dam group and the computed quadratic regression
Figure 6. Mean weaning weight of each age of dam group and the computed quadratic regression
weaning weight and the quadratic regressions fitted from the data. The curves would fit the data better if they rose more steeply for young cows and fell more slowly for older cows. A quadratic curve must be symmetrical around a line parallel to the y-axis. Therefore, age of dam was treated as a discrete variable in this analysis, since it was felt that the quadratic regression did not represent adequately the biology of the aging process. Since age of dam is a continuous variable the effect of age of dam could be represented by some curve. Fitting constants for age of dam by classes removes the variation which this curve would describe and also the variation due to real deviations of the group means from this hypothetical curve. This amounts to making the analysis within age of dam.

The following model was used for post-weaning gains:

\[ y_{ijkl} = \mu + c_i + s_j + a_k + h_{ik} + b(x_{ijkl} - \bar{x}_{ij}) + e_{ijkl} \]

The \( c_i, s_j \) and \( a_k \) are the effects of year, sex and age of dam, respectively. The \( h_{ik} \) is the interaction deviation of the \( i,k^{th} \) cell. The \( b \) is the regression on age of calf, \( x_{ijkl} \). Age of calf was taken as a deviation from the mean of the calf's year-sex group. Thus the regressions computed using this model were intra-year and intra-sex regressions.

The \( e \) contains all the remaining sources of variation which affect the trait but were not specified in the model.
Of course, any factor which was omitted and was not distrib-
uted evenly over the other variables biased the estimates of
them. The model for weaning weight contained a b for each
sex because the sex x age of calf interaction was important.
Birth weight was not included in this analysis because the
age of dam x year interaction was not significant for birth
weight.

The older age of dam classes were grouped so that ten
classes were considered. To solve the equations it was neces-
sary to absorb the $\mu + h_{1k}$ equations into the remaining equa-
tions.

The next step was to fit a model identical to the one
above except that the $h_{1k}$'s were omitted. This was done so
the age of dam x year interaction could be measured. The
interaction was significant ($P<.01$) for each trait except
gain in the fourth test period, for which the F ratio was
less than one.

By using the estimate of the sex difference and the age
of calf regression obtained from this analysis, the second
and fourth possibilities for explaining the interaction were
examined.

A large outside purchase of cows calved at two years of
age in 1951. They comprised about 70 per cent of their age
of dam group each year. This group was compared to their
age of dam-year contemporaries. The 109 calves from this
purchased group of cows weaned eight pounds lighter, on the average, than the 45 calves born to their contemporaries of the same age. Their calves were also eight pounds lighter than the average of all 748 calves, adjusted for age of calf and sex.

The difference between first and second calves born to three-year-old cows was of even greater importance. This difference at weaning was 25 pounds in favor of first calves born to three-year-old cows. All 21 three-year-old calvings from 1956 to 1958 were from first calf heifers. The 69 calves from three-year-olds prior to 1956 were mostly second calves although some were first calves also. Since the contrast was calves born from 1950 to 1955 vs. 1956 to 1958 the difference was probably larger than 25 pounds.

The following model was fitted in order to correct post-weaning gains for the environmental effects:

$$y_{ijklm} = \mu + c_i + s_j + a_k + d_1 + b(x_{ijklm} - \bar{x}_i) + e_{ijklm}$$

For weaning weight a separate b was estimated for each sex. For birth weight the b was omitted from the model. The notation is as described earlier except that $d_1$ has been added as the sire effect.

It was not possible to include both the age of dam x year interaction and sires in the same analysis. Except for birth weight, a separate parameter was included for the two groups of three-year-old cows. Sires were confounded to a large
degree with age of dam-year subgroups and the two groups of three-year-old cows were confounded with years. Including them in the analysis should account for some of the variation which was attributed to the interaction between year and ages of dam in the previous analysis. The remaining part of this variation would appear in the error sum of squares.

The constants for years, sexes, ages of dam and the age of calf regressions obtained from the above analysis are shown in Table 6. The data were corrected using these constants and the general formula:

\[ \text{corrected } y = y - \sum \hat{b} x. \]

For this to be accurate requires that no interactions existed between sires and the other variables. In addition, sires must have been uncorrelated with the other variables. Koch (1950) discussed the consequences of correlations among the variables in a least squares analysis.

Correcting the data for the year constants would have removed part of the genetic variation if genetic change was occurring in this herd through the years 1950 to 1958. The yearly means for the traits indicated little if any increase through this period. The age of dam constants for any trait were biased if cows remained in the herd because they were better genetically for that trait (Lush and Shrode, 1950).
Table 6. Environmental effects computed from the least squares analysis

<table>
<thead>
<tr>
<th>Year</th>
<th>Birth weight</th>
<th>Weaning weight</th>
<th>First period gain</th>
<th>Second period gain</th>
<th>Third period gain</th>
<th>Fourth period gain</th>
<th>Fifth period gain</th>
</tr>
</thead>
<tbody>
<tr>
<td>1950</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1951</td>
<td>-4.3</td>
<td>17.0</td>
<td>-13.7</td>
<td>11.9</td>
<td>16.5</td>
<td>12.4</td>
<td>-3.9</td>
</tr>
<tr>
<td>1952</td>
<td>-2.0</td>
<td>32.5</td>
<td>-12.1</td>
<td>9.2</td>
<td>32.6</td>
<td>24.4</td>
<td>27.2</td>
</tr>
<tr>
<td>1953</td>
<td>-1.5</td>
<td>17.1</td>
<td>-13.3</td>
<td>15.1</td>
<td>18.1</td>
<td>17.9</td>
<td>19.5</td>
</tr>
<tr>
<td>1954</td>
<td>-7.3</td>
<td>25.0</td>
<td>7.7</td>
<td>21.1</td>
<td>24.0</td>
<td>6.5</td>
<td>16.7</td>
</tr>
<tr>
<td>1955</td>
<td>-3.2</td>
<td>44.9</td>
<td>-5.4</td>
<td>-2.0</td>
<td>2.6</td>
<td>5.9</td>
<td>8.2</td>
</tr>
<tr>
<td>1956</td>
<td>-4.8</td>
<td>10.0</td>
<td>-21.1</td>
<td>-2.3</td>
<td>17.9</td>
<td>15.7</td>
<td>15.2</td>
</tr>
<tr>
<td>1957</td>
<td>-1.2</td>
<td>10.0</td>
<td>-40.4</td>
<td>-.9</td>
<td>37.8</td>
<td>33.4</td>
<td>9.8</td>
</tr>
<tr>
<td>1958</td>
<td>-0.2</td>
<td>7.6</td>
<td>-5.4</td>
<td>-3.5</td>
<td>8.0</td>
<td>7.0</td>
<td>11.0</td>
</tr>
</tbody>
</table>

Age of dam
- 3 (1st calf)
- 4
- 5-7
- 8-12
- 13-17

Sex
- Bulls
- Heifers

Age of calf
- Bulls
- Heifers
- Bulls and heifers

| Age | Bulls | Heifers | 2.0 | 1.4 | 0.11 | 0.08 | 0.04 | 0.02 | 0.01 |
Genetic Analysis

A paternal half-sib analysis was made on the corrected data. The analyses of variance and covariance (Hazel et al., 1943) are illustrated in Table 7. No allowance was made for the degrees of freedom used in computing the environmental constants from the data. Since these were not distributed

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Expected mean square</th>
<th>Expected covariance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sires</td>
<td>s-1</td>
<td>V(A_i) + k V(S_1)</td>
<td>cov(A_i,A_j) + k cov(S_1,S_j)</td>
</tr>
<tr>
<td>Half-sibs</td>
<td>Σ(n_i - 1)</td>
<td>V(A_1)</td>
<td>cov(A_i,A_j)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>n_i = number of calves by the i_th sire</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>n. = Σ n_i</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>k = (n. - Σ n_i^2/n.) / (s-1)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

exactly proportionately among the sires, the components of variance and covariance were biased to some extent. An analysis by Sutherland (1958) indicates that this bias would be of minor importance.

The simplest model that can be assumed is

\[ P = G + E \]

where \( P \) is the phenotype for a trait, \( G \) is the sum of the
additive effects of the genes affecting the trait and $E$ is the environmental contribution plus the dominance and epistatic contributions to the phenotype.

The $V(S)$ is the covariance between paternal half-sibs. If mating is random and the environmental correlation between members of a sire's progeny is zero, the genic relationship among half-sibs is one-fourth and the genic variance in the population may be estimated by $4V(S)$. Actually, if the differences between the progeny group means are entirely genetic, $V(S)$ would be expected to contain $1/4 \ V(G)$ plus $1/16$ of the variance due to two-loci interactions, $1/64$ of that due to three-loci interactions, etc. of the additive effects of the loci (Kempthorne, 1957). If the sires were a group selected for any particular trait the variance among the sires in the unselected population would be underestimated for that trait. This bias would be small unless heritability was very high and the selection for it had been intense. This simple multiplication of the sire component further assumes that each sire is mated to a group of randomly chosen cows.

For brevity $G$ will be referred to as genic and $E$ as environmental remembering the above qualifications. If $G$ and $E$ are uncorrelated the following relations hold:

\[
\begin{align*}
V(P) &= V(G) + V(E) \\
V(P) &= V(A) + V(S) \\
V(G) &= 4V(S) \\
V(E) &= V(A) - 3V(S)
\end{align*}
\]
and similarly for the covariances

\[ \text{cov}(P_i, P_j) = \text{cov}(A_i, A_j) + \text{cov}(S_i, S_j) \]

\[ \text{cov}(G_i, G_j) = 4 \text{cov}(S_i, S_j) \]

\[ \text{cov}(E_i, E_j) = \text{cov}(A_i, A_j) - 3 \text{cov}(S_i, S_j). \]

From the variances and covariances computed from the data, heritability and the phenotypic, genic and environmental correlations were calculated by the following formulae:

\[ h^2 = \frac{\text{V}(G)}{\text{V}(P)} \]

\[ r_{P_iP_j} = \frac{\text{cov}(P_i, P_j)}{\left[ \text{V}(P_i) \text{V}(P_j) \right]^{1/2}} \]

\[ r_{G_iG_j} = \frac{\text{cov}(G_i, G_j)}{\left[ \text{V}(G_i) \text{V}(G_j) \right]^{1/2}} \]

\[ r_{E_iE_j} = \frac{\text{cov}(E_i, E_j)}{\left[ \text{V}(E_i) \text{V}(E_j) \right]^{1/2}} \]

Table 8 contains the heritabilities computed from the data. The heritabilities of total gain on feed \( (P_8 = \sum_{i=3}^{7} P_i) \) and final weight \( (P_9 = \sum_{i=2}^{7} P_i) \) were computed by adding the appropriate genic and phenotypic variances and covariances. For example,

\[ \text{V}(G_8) = \sum_{i=1}^{1} \text{V}(G_i) + \sum_{i \neq j}^{1,7} \text{cov}(G_i, G_j) \]

\[ i \text{ and } j = 3 \text{ to } 7 \]

Table 9 contains the phenotypic, genic and environmental correlations among the seven traits. Correlations exceeding
Table 8. Heritabilities and their approximate standard errors

<table>
<thead>
<tr>
<th>Trait</th>
<th>Symbol</th>
<th>$h^2$</th>
<th>$s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth weight</td>
<td>$P_1$</td>
<td>.22</td>
<td>.10</td>
</tr>
<tr>
<td>Weaning weight</td>
<td>$P_2$</td>
<td>.25</td>
<td>.11</td>
</tr>
<tr>
<td>First period gain</td>
<td>$P_3$</td>
<td>.18</td>
<td>.09</td>
</tr>
<tr>
<td>Second period gain</td>
<td>$P_4$</td>
<td>.28</td>
<td>.11</td>
</tr>
<tr>
<td>Third period gain</td>
<td>$P_5$</td>
<td>.18</td>
<td>.08</td>
</tr>
<tr>
<td>Fourth period gain</td>
<td>$P_6$</td>
<td>.08</td>
<td>.06</td>
</tr>
<tr>
<td>Fifth period gain</td>
<td>$P_7$</td>
<td>.04</td>
<td>.05</td>
</tr>
<tr>
<td>Total feedlot gain</td>
<td>$P_8$</td>
<td>.40</td>
<td>.14</td>
</tr>
<tr>
<td>Final weight</td>
<td>$P_9$</td>
<td>.47</td>
<td>.16</td>
</tr>
</tbody>
</table>

Unity may, of course, occur because of sampling errors when correlations are computed from variance and covariance components.

Figure 7 is a path coefficient diagram (Wright, 1934) illustrating the relations assumed to exist between the genic and environmental sources of phenotypic variation. The phenotypic correlation is the sum of the genic and environmental constituents as follows:

$$r_{P_iP_j} = h_i r_{G_iG_j} h_j + e_i r_{E_iE_j} e_j$$

Using the formula given by Fisher (1954) for the sampling error of an intraclass correlation, the sampling error for
### Table 9. Phenotypic, genic and environmental correlations

<table>
<thead>
<tr>
<th></th>
<th>P_2</th>
<th>P_3</th>
<th>P_4</th>
<th>P_5</th>
<th>P_6</th>
<th>P_7</th>
<th>P_8</th>
<th>P_9</th>
</tr>
</thead>
<tbody>
<tr>
<td>P_1</td>
<td>phen.</td>
<td>.31</td>
<td>.14</td>
<td>.14</td>
<td>.11</td>
<td>.15</td>
<td>.11</td>
<td>.26</td>
</tr>
<tr>
<td></td>
<td>gen.</td>
<td>.69</td>
<td>.94</td>
<td>1.04</td>
<td>.12</td>
<td>1.03</td>
<td>.12</td>
<td>.25</td>
</tr>
<tr>
<td></td>
<td>env.</td>
<td>.19</td>
<td>-0.05</td>
<td>-0.16</td>
<td>.10</td>
<td>0.02</td>
<td>.11</td>
<td>.01</td>
</tr>
<tr>
<td>P_2</td>
<td>phen.</td>
<td>.11</td>
<td>.22</td>
<td>.11</td>
<td>.14</td>
<td>.02</td>
<td>.24</td>
<td>.87</td>
</tr>
<tr>
<td></td>
<td>gen.</td>
<td>1.21</td>
<td>.93</td>
<td>.82</td>
<td>.75</td>
<td>-0.25</td>
<td>.93</td>
<td>.98</td>
</tr>
<tr>
<td></td>
<td>env.</td>
<td>-0.19</td>
<td>-0.04</td>
<td>-0.02</td>
<td>0.03</td>
<td>0.05</td>
<td>-0.08</td>
<td>.84</td>
</tr>
<tr>
<td>P_3</td>
<td>phen.</td>
<td>.06</td>
<td>-0.01</td>
<td>.01</td>
<td>.01</td>
<td>.47</td>
<td>.32</td>
<td></td>
</tr>
<tr>
<td></td>
<td>gen.</td>
<td>1.06</td>
<td>.51</td>
<td>.74</td>
<td>.27</td>
<td>.94</td>
<td>1.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>env.</td>
<td>-0.22</td>
<td>-0.12</td>
<td>-0.08</td>
<td>-0.02</td>
<td>.31</td>
<td>.00</td>
<td></td>
</tr>
<tr>
<td>P_4</td>
<td>phen.</td>
<td>.08</td>
<td>.03</td>
<td>.48</td>
<td>.41</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>gen.</td>
<td>.87</td>
<td>.19</td>
<td>.93</td>
<td>.95</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>env.</td>
<td>-0.06</td>
<td>.02</td>
<td>.28</td>
<td>.11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P_5</td>
<td>phen.</td>
<td>.06</td>
<td>.17</td>
<td>.48</td>
<td>.33</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>gen.</td>
<td>.88</td>
<td>.74</td>
<td>.74</td>
<td>.69</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>env.</td>
<td>-0.06</td>
<td>.17</td>
<td>.41</td>
<td>.20</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P_6</td>
<td>phen.</td>
<td>.19</td>
<td>.53</td>
<td>.37</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>gen.</td>
<td>.82</td>
<td>1.00</td>
<td>.88</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>env.</td>
<td>.15</td>
<td>.45</td>
<td>.27</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P_7</td>
<td>phen.</td>
<td>.54</td>
<td>.29</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>gen.</td>
<td>.46</td>
<td>.08</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>env.</td>
<td>.63</td>
<td>.39</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P_8</td>
<td>phen.</td>
<td>.69</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>gen.</td>
<td>.98</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>env.</td>
<td>.47</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

heritability computed from a half-sib analysis is

\[
\frac{32 (1-t)^2}{(s-1) n(n-1)} \left[ 1 + \frac{(n-1) t}{s-1} \right]^2
\]

where \( t \) is the observed intraclass correlation, \( s \) is the number of sires and \( n \) is the number of calves per sire.
Figure 7. Path coefficient diagram illustrating the relations among the genic (G) and environmental (E) contributions to the correlation between phenotypes (P).
\[ h = \frac{\sigma_G}{\sigma_P} \]

\[ e = \frac{\sigma_E}{\sigma_P} \]
The approximate standard errors of the heritabilities were calculated using this formula and are shown in Table 8. These are approximate because the number of calves per sire varied, but the average was used to compute these variances. The standard errors for \( P_8 \) and \( P_9 \) were computed by considering the intraclass correlation was to be one-fourth of heritability.

Robertson (1959) gave the following formula for the sampling error of a genetic correlation coefficient where heritabilities of the two traits were equal.

\[
\frac{1}{n^2 t^2} \left\{ \left[ nt(1-r_{GG}^2) + (1-t)(1-r_{GG} r_{AA}) \right]^2 + (1-t)^2 (r_{GG} - r_{AA})^2 \right\} / (s-1) + \left[ (1-t)^2 (r_{GG} - r_{AA})^2 + (1-r_{GG} r_{AA})^2 \right] / s(n-1)
\]

In this formula \( t \) is the intraclass correlation for both traits and \( r_{AA} \) is the correlation between the two traits in the same individual within progeny groups. By substituting values typical of the present data it was possible to compute a sampling variance which would give some idea of the sampling variances of the genic correlations computed from these data. Assuming values of \( t = .05 \), \( r_{GG} = .5 \), \( r_{AA} = .1 \), \( s = 23 \) and \( n = 34 \), the sampling variance was .0773, the standard error being .28. This suggests that with the numbers available in this study the genic correlations would occasionally exceed one, or be lower than zero, if the true parameter was .5.
The genetic improvement expected from selection (assuming a linear relationship between the variables) is

$$\Delta G = r_{GI} \left[ \frac{V(G)}{V(I)} \right]^{1/2} (I_s - I_p).$$

Here $I$ is the variable used as a basis for selection, $I_p$ is the mean of the unselected population and $I_s$ is the mean of the animals selected to be parents. The change in $G$ is proportional to $r_{GI}$ (Lush, 1948).

Let $G_t = \sum G_i$ be the sum of the average effects of the genes for final weight. Then $G_t$ may be predicted by $I$ where $I$ is an index containing one or more phenotypic characters giving information about $G_t$. The index is simply the multiple regression equation $I = \sum \hat{b}_1 P_1$. In terms of the notation ordinarily used in multiple regression, $G_t$ is $y$ and $I$ is $\hat{y}$ such that $G_t = I + e$. This differs from the usual multiple regression problem in that $G_t$ cannot be measured directly.

The equations which maximize $r_{GI}$ are the least squares equations which minimize $\sum (G_t - I)^2$. The equations are

$$\hat{b}_1 V(P_1) + \hat{b}_2 \text{cov}(P_1, P_2) + \ldots = \text{cov}(G_t, P_1)$$

$$\hat{b}_1 \text{cov}(P_1, P_2) + \hat{b}_2 V(P_2) + \ldots = \text{cov}(G_t, P_2)$$

$$\vdots$$

where $\text{cov}(G_t, P_1) = \text{cov}(G_t, G_1 + E_1)$. If $\text{cov}(G_t, E_1) = 0$, then $\text{cov}(G_t, P_1) = V(G_1) + \sum_j \text{cov}(G_1, G_j)$. These relationships
were given by Hazel et al. (1943). Only the genic and phenotypic variances and covariances are needed to solve the equations. These, as computed from the data of the present study, are shown in Table 10.

In order to compute $r_{G_tI} = \frac{\text{cov}(G_t, I)}{\sqrt{\text{V}(I) \text{V}(G_t)}}$ the following relations are necessary:

$$\text{cov}(G_t, I) = \text{cov}(\sum G_i, \sum \hat{b}_i P_i)$$

$$= \sum_i \hat{b}_i \text{cov}(P_i, G_i) + \sum_{i \neq j} \hat{b}_i \text{cov}(P_i, G_j)$$

and

$$\text{V}(I) = \sum_i \hat{b}_i \text{cov}(G_t, P_i)$$

$$= \sum_i \hat{b}_i \text{cov}(P_i, G_i) + \sum_{i \neq j} \hat{b}_i \text{cov}(P_i, G_j)$$

so

$$r_{G_tI} = \sqrt{\frac{\text{V}(I)}{\text{V}(G_t)}}$$

where

$$\text{V}(G_t) = \sum_i \text{V}(G_i) + \sum_{i \neq j} \text{cov}(G_i, G_j).$$

The change in the sum of the average effects of the genes ($G_t$) which is achieved by selection on an index ($I$) is proportional to the correlation between $G_t$ and the index predicting $G_t$. Therefore this correlation is useful in comparing the indices. For final weight $G_t = \sum_{i=2}^{7} G_i$ since final weight is weaning weight plus gain in all five feeding periods. The standard deviation of $G_t$ was 55.1.
Table 10. Phenotypic and genic variances and covariances

<table>
<thead>
<tr>
<th></th>
<th>( P_1 )</th>
<th>( P_2 )</th>
<th>( P_3 )</th>
<th>( P_4 )</th>
<th>( P_5 )</th>
<th>( P_6 )</th>
<th>( P_7 )</th>
<th>( P_8 )</th>
<th>( P_9 )</th>
</tr>
</thead>
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<td>164.35</td>
<td>23.23</td>
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<td>15.23</td>
<td>22.28</td>
<td>14.70</td>
<td>95.35</td>
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<tr>
<td></td>
<td>gen.</td>
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<td>86.00</td>
<td>29.84</td>
<td>37.48</td>
<td>3.44</td>
<td>20.40</td>
<td>1.48</td>
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<td>3570.29</td>
<td>115.20</td>
<td>214.27</td>
<td>105.70</td>
<td>131.95</td>
<td>20.55</td>
<td>587.67</td>
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<td>276.92</td>
<td>241.60</td>
<td>124.60</td>
<td>107.08</td>
<td>-22.12</td>
<td>727.48</td>
<td>1626.16</td>
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<td>phen.</td>
<td>322.87</td>
<td>17.68</td>
<td>-1.55</td>
<td>2.82</td>
<td>1.31</td>
<td>350.13</td>
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<td>25.88</td>
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<td>7.79</td>
<td>323.62</td>
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<tr>
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<td>35.52</td>
<td>4.68</td>
<td>209.36</td>
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<td>gen.</td>
<td>45.16</td>
<td>28.12</td>
<td>4.76</td>
<td>129.44</td>
<td>254.04</td>
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<td>11.39</td>
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</table>
The regression of $G_t$ on each of the seven traits and the correlation between each trait and $G_t$ are shown in Table 11 (I₁ to I₇). In order to investigate whether the feeding period might be shortened six indices (I₈ to I₁₃) were computed, adding the traits successively as they would become available in a testing program. These indices and their correlations with $G_t$ are also given in Table 11. Five indices (I₁₄ to I₁₈) were computed successively adding the traits as before but omitting birth weight (Table 11). This was done to see if birth weight might be omitted with little loss of accuracy in predicting $G_t$.

Indices predicting the genic effects for gain in the entire 140-day period were calculated where $G'_t = \sum_{i=3}^{7} G_i$. Thus $G'_t$ differs from $G_t$ only that it does not include weaning weight. The regression coefficients and correlations between $G'_t$ and the seven traits individually (I₁ to I₇) are shown in Table 12. Three indices were calculated predicting $G'_t$ from birth weight and weaning weight (I₈'), gain in the first 84 days (I₉') and gain in the entire 140-day period (I₁₀'). These indices and their correlations with $G'_t$ are given in Table 12. The standard deviation of $G'_t$ was 26.2.
Table 11. Regression coefficients for the indices predicting the genic effects for final weight ($G_t$) and the correlations between $G_t$ and each index

<table>
<thead>
<tr>
<th>Index</th>
<th>$F_1$</th>
<th>$F_2$</th>
<th>$F_3$</th>
<th>$F_4$</th>
<th>$F_5$</th>
<th>$F_6$</th>
<th>$F_7$</th>
<th>(\sqrt{V(I)})^{1/2}</th>
<th>$r_{G_tI}$</th>
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</thead>
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<tr>
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<td>.46</td>
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</tr>
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<td>1.67</td>
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<td>43.4</td>
<td>.79</td>
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<tr>
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<td>1.29</td>
<td>.82</td>
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<td></td>
<td></td>
<td>44.3</td>
<td>.80</td>
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<tr>
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<td>1.30</td>
<td>.86</td>
<td>.60</td>
<td>-.29</td>
<td></td>
<td>44.5</td>
<td>.81</td>
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</tbody>
</table>
Table 12. Regression coefficients for the indices predicting the genic effects for total feedlot gain \( (G_t) \) and the correlations between \( G_t \) and each index

<table>
<thead>
<tr>
<th>Index</th>
<th>( p_1 )</th>
<th>( p_2 )</th>
<th>( p_3 )</th>
<th>( p_4 )</th>
<th>( p_5 )</th>
<th>( p_6 )</th>
<th>( p_7 )</th>
<th>( \sqrt{V(I)} )</th>
<th>( r_{G_t,I} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( I_1 )</td>
<td>1.15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
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<td>( I_2 )</td>
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<td></td>
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<td></td>
<td>.46</td>
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</tr>
<tr>
<td>( I_3 )</td>
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<td></td>
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<td>.49</td>
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<tr>
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<td>.31</td>
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<td>.46</td>
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<td>14.1</td>
<td>.54</td>
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<tr>
<td>( I_9 )</td>
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<td>.73</td>
<td>.49</td>
<td></td>
<td></td>
<td></td>
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<td>17.8</td>
<td>.68</td>
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<td>.38</td>
<td>-.04</td>
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<td></td>
<td>18.8</td>
<td>.72</td>
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</tbody>
</table>
Environmental Analysis

Interactions between environmental factors

Landblom (1954) made tests of significance about the three two-factor interactions and the three-factor interaction, involving sex, age of dam and year, for weaning weight. She computed the sum of squares for interaction by multiplying the number in each subclass by the squared difference between the actual and expected subclass means and summing these over all subclasses. The expected subclass means were constructed from constants obtained by fitting the main effects. Thus the sum of squares for each two-factor interaction was computed ignoring the other variable. The residual mean square after removing only the main effects was used in the denominator of the $F$ ratio for testing the interactions. Unless the interactions were negligible this residual mean square would be too large and the $F$ values obtained would be smaller than the correct ones. Only the interaction of sex and age of dam yielded a significant $F$ value. The computed $F$ value was 2.13, whereas significance at the five percent level required only 2.12. Dahmen and Bogart (1952) found an exceedingly small sex x year interaction for daily gain.

The methods employed in this study were approximate, as is often necessary when applying statistics to large animal
data. The biologist must attempt to ascertain whether or not the approximations he uses affect seriously the reliability of his estimates.

The graphs showing the interaction of sex and year (e.g. Figure 4) clearly indicated that the contribution of this source of variation to the total sum of squares, though not determined by the analysis, would be small.

When many tests of significance are made at the five percent level, one in 20 should be significant by chance. One cannot distinguish those based on real differences from those that happened by chance. Since 32 tests were made about the interactions, it is probable that at least one and perhaps three might have been significant due to chance. What one would really like to know is what fraction of the total variance is contributed by each interaction.

The F ratios for all of the traits for the interactions between age of calf and age of dam and also between age of calf and year were smaller than required for the five percent probability level of significance. Therefore it seems consistent to assume these interactions were not important. The interaction of age of dam with sex was barely significant for the third gain period and was well below the five percent probability level for the other traits. Since this interaction was not consistently important it was disregarded.

The interaction of age of calf and sex was highly sig-
significant for weaning weight. It is generally known that bulls grow faster than heifers prior to weaning. This is apparent from the larger sex difference for weaning weight than for birth weight. Weaning weight was corrected for this interaction by fitting a regression on age of calf for each sex separately. The only other trait for which the age of calf x sex interaction was significant was gain in the last period. Since it did not seem logical to fit separate regressions for one of the gain periods and not for the others, a single regression was fitted for post-weaning gains.

The most surprising result concerning the interactions was the large interaction of age of dam and year. This was significant for weaning weight and for gain in the first, third and fifth periods. The interaction was tested again for weaning weight and post-weaning gain by treating age of dam as a discontinuous variable. Sex and age of calf were included in this analysis. For gain in the fourth period this interaction was not significant but for the other traits it was significant at the one percent level. Since sires were confounded to some degree with age of dam - year subclasses, including sires in the final analysis should have removed part of the variation previously attributed to the interaction between age of dam and year. Including separate equations for three-year-old cows calving for the first and second times should have reduced further the variation due to this inter-
action. The remaining sum of squares which had been attributed to the interaction would be in the error.

After examining the data with the intent of finding factors which contributed to the sum of squares for the interaction between age of dam and year, and then removing these contributions, there seemed no point in making further tests of significance about this interaction. The analysis did not satisfactorily determine how important the interaction between age of dam and year really was. Since this interaction was ignored in the analysis used to compute the environmental constants the data were not corrected for it.

Effect of sex

The sex difference for birth weight, computed by the least squares analysis, was 3.9 pounds. This is smaller than most values given in the literature for beef cattle but is within the range reported (Table 13). The sex difference for weaning weight was 45.4 pounds which is within the range reported by other workers (Table 14) for bulls minus heifers. The sex differences for gain in the five feeding periods were 2.2, 8.4, 8.8, 11.3 and 10.4, respectively, the bulls always gaining more than the heifers on the average. Summing and dividing by 140 days gives .29 pounds as the sex difference for average daily gain over the entire feeding period. Dahmen and Bogart (1952) found a difference of .3 between
Table 13. Differences in birth weight for bull and heifer calves as reported in the literature

<table>
<thead>
<tr>
<th>Bulls-heifers in pounds</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.8</td>
<td>Burris and Blunn (1952)</td>
</tr>
<tr>
<td>4.2</td>
<td>Dawson et al. (1947)</td>
</tr>
<tr>
<td>5.0</td>
<td>Gregory et al. (1950)</td>
</tr>
<tr>
<td>4.7</td>
<td>Knapp et al. (1940)</td>
</tr>
<tr>
<td>5.6</td>
<td>Koch and Clark (1955a)</td>
</tr>
<tr>
<td>5.2</td>
<td>Koch et al. (1959)</td>
</tr>
<tr>
<td>3.5</td>
<td>Nelms and Bogart (1956)</td>
</tr>
<tr>
<td>4.2</td>
<td>Woolfolk and Knapp (1949)</td>
</tr>
</tbody>
</table>

average daily gain for bulls and heifers.

Effect of age of dam

The average birth weight for each age group of dams and the quadratic regression computed from the uncorrected data were shown in Figure 5. Figure 8 shows for each age of dam class the constant obtained from the least squares analysis (Table 6), plotted against the average age of the cows for which the constant was computed. Probably no direct selection was practiced on the cows based on the birth weight of their calves. However, the constants for the older age groups were biased if a positive genetic correlation existed between birth
Table 14. Differences in weaning weight for bull, steer and heifer calves as reported in the literature

<table>
<thead>
<tr>
<th>Pounds</th>
<th>Kind of comparison</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.0</td>
<td>S-H(^a)</td>
<td>Brinks (1957)</td>
</tr>
<tr>
<td>23.0</td>
<td>B-H</td>
<td>Burgess et al. (1954)</td>
</tr>
<tr>
<td>5.0</td>
<td>S-H</td>
<td>Gregory et al. (1950)</td>
</tr>
<tr>
<td>43.8</td>
<td>B-H</td>
<td>Koch (1951)</td>
</tr>
<tr>
<td>26.2</td>
<td>B and S-H</td>
<td>Koch and Clark (1955a)</td>
</tr>
<tr>
<td>32.0</td>
<td>S-H</td>
<td>Koger and Knox (1945)</td>
</tr>
<tr>
<td>68.0</td>
<td>B-H</td>
<td>Rollins and Guilbert (1954)</td>
</tr>
<tr>
<td>31.0</td>
<td>S-H</td>
<td>Rollins and Wagnon (1955)(^b)</td>
</tr>
<tr>
<td>18.0</td>
<td>S-H</td>
<td>Rollins and Wagnon (1956)(^c)</td>
</tr>
<tr>
<td>28.0</td>
<td>B-H</td>
<td>Woolfolk and Knapp (1949)</td>
</tr>
</tbody>
</table>

\(^a\)B - bulls; S - steers; H - heifers.

\(^b\)Optimum nutrition.

\(^c\)Sub-optimum nutrition.

weight and some other trait for which cows were culled on the basis of their calves' performance. The effects of age of dam on birth weight in these data were similar to those reported in the literature (Table 15). According to Dawson et al. (1947), the average birth weight increased until the cows were six years of age. This average then remained about the same from six to ten years of age but decreased for
Figure 8. Least squares constants for the effect of age of dam on birth weight

Figure 9. Least squares constants for the effect of age of dam on weaning weight
Table 15. Effects of age of dam on birth weight as reported in the literature

<table>
<thead>
<tr>
<th>Age of dam</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Koch and Clark (1955a)</td>
</tr>
<tr>
<td>2</td>
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<tr>
<td>4</td>
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<td>-2</td>
</tr>
<tr>
<td>11</td>
<td>-5</td>
</tr>
</tbody>
</table>

11-year-old cows.

Since age of dam is a continuous variable, a continuous curve representing the effect of age of dam must exist for any given set of environmental conditions. One would expect the shape of this curve to be different in Ohio and in the range states. For example, this would be so if older cows were more seriously handicapped on the range where good teeth and extensive traveling are more essential for obtaining food.
than in Ohio. Also the shape of the curve might be different for the various traits.

Figure 5 shows the average weaning weight of calves from cows of each age group and the quadratic regression computed from the data. Figure 9 shows the least squares constants (Table 6) for the effect of age of dam on weaning weight. The constant for first calves from three-year-old cows is not shown on this graph. These constants are biased to the extent that selection of the cows for the weaning weight of their calves was effective. Table 16 contains the effects of age of dam on weaning weight, as reported in other studies.

In those studies the cows from six to eight years of age weaned the heaviest calves. In the present data eight- to 12-year-old cows produced the heaviest calves. This difference could be due either to the management and environment of this herd or the effectiveness of selection here may have raised the weaning weights for the older cows. Selection could have biased the values for some of the studies listed in Table 16 also. Koch and Clark (1955a) attempted to remove this bias. Certainly age was not as severe a handicap in this herd as it is under range conditions. Brinks' (1957) data, which were from the Michigan State University herd, are fairly similar in magnitude to the present data if the Michigan seven-year-old cows were low by chance. The conditions under
Table 16. Effects of age of dam on weaning weight as reported in the literature

<table>
<thead>
<tr>
<th></th>
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<td></td>
<td>-51</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

*aOptimum nutrition.

*bSub-optimum nutrition.

which the Michigan calves were raised would be more similar to Ohio conditions than would those of the other studies in Table 16. Probably both selection and environment are responsible for the high values obtained for the older cows.

Figure 10 shows the least squares constants for the effects of age of dam on gain in the first period. The tendency for this curve to be concave upwards seems to demon-
Figure 10. Least squares constants for the effect of age of dam on first period gain

Figure 11. Least squares constants for the effect of age of dam on 140-day gain
strate compensatory gain. That is, calves from both young and old cows received less milk, on the average, than calves from middle-aged cows. The calves receiving less milk prior to weaning made larger gains on feed in the first 28 days following weaning. The constants in Table 6 show that the effect of age of dam was slightly concave upwards for the second 28 days of the feeding period but became convex upwards for the last three periods.

The net effect of the age of dam on the total of the five periods is shown in Figure 11. In Figure 11 the sum of the constants for all five periods are plotted. Clearly the age of dam affects the post-weaning gains and should be considered when evaluating an individual's performance on a feeding test. Because of the way in which the effect of age of dam changed through the feeding test, the effect on the total feeding period would have been quite different if the feeding test had been less than 140 days. Also it seems likely this effect would have been different if the test had been of still longer duration.

Effect of age of calf

The age of calf, like the age of dam, would be expected to have different effects in different environments. Most workers have found age of calf to affect weaning weight nearly linearly (Brinks, 1957; Burgess et al., 1954; Koch, 1951;
Lush, 1930; Marlowe and Gaines, 1958). In most of these studies the effect of age of calf decreased slightly for older calves. The particular age at which this occurred varied in the different studies. Johnson and Dinkel (1951) found linear growth to 155 days. At 155 days the rate of growth decreased sharply but growth from 155 to 225 days was nearly linear also. The authors concluded that using two separate linear adjustments (i.e. one for 0 to 154 days and another for 155 to 225 days) was more accurate than correcting the weights by a quadratic curve fitted from 0 to 225 days.

The most serious error in using a linear correction in the present data was that it overcorrected the older calves. This was because the actual effect of age was less after about 240 days (Figure 1). Plotting weaning weight against weaning age separately for bulls and heifers showed that the effect of age was nearly linear till about 240 days and decreased after that for each sex.

The average daily gain from birth to weaning was 1.61 pounds for bulls and 1.46 pounds for heifers. The least squares regressions were 2.03 pounds for bulls and 1.35 pounds for heifers. These least squares regressions were based on the range in age of calf at weaning represented in the data. In these data the range was from 124 to 286 days. The differences between the least squares regressions and the
average daily gains indicate that the bulls were growing at a faster rate during the period just prior to weaning than they were earlier, while the heifers grew more slowly just prior to weaning than they had grown earlier.

The effect of the age of calf at weaning on post-weaning gains decreased for each successive 28-day period. The regressions for the five periods, in order of their occurrence, were .11, .08, .04, .02 and .01. These regressions are in pounds of gain for the 28-day period per day of age at the beginning of the test. If the calves were growing linearly from weaning onward the regressions would be zero.

The data were corrected for sex, year, age of dam and age of calf using the least squares constants. Any errors in estimating the environmental effects would have some effect on the genetic and phenotypic variances and covariances obtained from the paternal half-sib analysis. Not correcting for the interaction of age of dam and year (if it were real) would have increased the variance within sires, provided sires were not confounded with age of dam - year subclasses. If the sires were confounded with these subclasses the variance between sires still should not be biased. If the year constants included something from genetic trend and were not wholly genetic, genetic differences between cows would seem less than they really were, and the variation within sires would be biased down. The year constants in Table 6 indicate that
no phenotypic trend existed for any trait. To infer that no genetic trend existed one must assume that no environmental trend occurred.

Some of the real differences between cows would have been removed if the constants for age of dam were biased by the cows having been selected on performance of their calves. Again this would have decreased the variance between half-sibs. If some sires were usually mated to old cows and other sires were mated to young cows the variance between sires would be biased upward by such consistent differences between the mates of one sire and the mates of another. Adjusting weaning weight for age by a linear regression probably over-corrected the older calves. This would tend to reduce the variation in weaning weight. The variance between half-sibs would be biased down and the variance between sires would be unbiased unless some sires consistently sired calves reaching an age of over 240 days at weaning.

Genetic Analysis

Analyses of variance and covariance

Estimating the additive genetic or genic variance by the correlation between paternal half-sibs was discussed by Lush (1948). Use of this method assumed there were no environmental correlations among the paternal half-sibs. Such a correlation would bias the component of variance for sires
up, but the covariance between sires could be biased in either direction. Correcting the data for differences between years should have removed the environmental correlation resulting from the sires being used in different years. Cows which were bred to a particular sire were subjected to the same environment during the breeding season because pasture matings were made. If the sire was mated to the same group of cows the next year his progeny from the previous matings would be raised to weaning in the same pasture. Any environmental correlation among a sire's progeny must have been induced prior to weaning unless they were predominantly of one sex, because all the bull calves were together in one pen and all the heifer calves in a different pen after weaning. The moderately small components of variance between sires seem to indicate that environmental correlations between paternal half-sibs were not large in these data. Presumably four times the component between sires contains at least a little from heritability so not much remains to be accounted for by environmental correlations.

Both sampling error and any bias due to environmental correlations are multiplied by the reciprocal of the coefficient of relationship among the paternal half-sibs. If there is no inbreeding and if the dams are unrelated this relationship is one-fourth. The relationship was undoubtedly at least a little larger in these data since a few calves were
full-sibs. Since the owner was intentionally avoiding inbreeding, there would be a tendency for sires to mate with cows more closely related to each other than the average of the group. This would further increase the relationship among half-sibs. This would make the variance and covariance components for sires a little larger than if they were only and exactly half-sibs.

The average relationship among the progeny was computed, taking into account full-sib relationships but ignoring other maternal relationships. This value was .253. Therefore ignoring the full-sib relationships was not a serious error. Relationships among different cows bred to the same bull would also increase the average relationship among a sire's progeny. Also if the epistatic variance due to the interaction of additive effects of two or more loci was large, the variance between sires would contain a little of this in addition to one-fourth of the additive variance. If the sires were more similar genetically than the population of sires for any trait, the component of variance for sires for that trait would be slightly too small.

The correlation between the dominance deviations of half-sibs is zero if no inbreeding has occurred. The average correlation between the dominance deviations of the members of a sire's progeny would be a little larger than zero in this study, because relationships existed among the cows bred to a
particular sire. This discrepancy is of minor importance.

Both the variance and covariance components for sires should be unbiased by maternal effects in a paternal half-sib analysis.

The relationships assumed to compute the genic and environmental variances and covariances were shown in Figure 7. This diagram assumed that no correlation existed between $G$ and $E$. For a correlation between genotype and environment to exist, animals with the better genotypes would have been consistently exposed to better or worse environments. The milk production of the cow is environment for the calf. Also the calf receives half his genes from his dam (ignoring sex-linkage). If a genic correlation between milking ability and gain existed, a correlation between genotype and environment would have existed for weaning weight of the calves. However, this should not have biased the variance or covariance between sires, assuming that the sires were mated to groups of cows of equal merit. It was assumed that $V(P) = V(G) + V(E)$, and $V(E)$ was computed as $V(P) - V(G)$. Hence if a correlation between $G$ and $E$ existed, $V(E)$ would be biased by $2 \text{cov}(G,E)$. This bias could be in either direction depending on the sign of the correlation. If a negative genic correlation between milking ability and pre-weaning gains existed as Koch (1953) suggested, $V(E)$ as computed here was too small. The amount of this bias could be determined
if the necessary information were known. An example is presented below to illustrate this bias.

Figure 12 is a path diagram showing the necessary relationships. The following symbols are used in Figure 12:

- $G_w^i$ - genotype of dam for weaning weight
- $G_m^i$ - genotype of dam for maternal environment
- $P_m^i$ - phenotype of dam for maternal environment
- $G_w$ - genotype of calf for weaning weight
- $P_w$ - phenotype of calf for weaning weight
- $E_w$ - environment of calf for weaning weight other than $P_m^i$

Koch (1953) suggested that the genetic correlation between maternal environment for pre-weaning gain and pre-weaning gain was about -.6. In order to illustrate the problem we will assume this value applies to weaning weight. It is also necessary to assume arbitrary values for the paths from $G_m^i$ to $P_m^i$ and $P_m^i$ to $P_w$. Then the correlation between the calf's genotype for weaning weight and the dam's phenotype for maternal effect is $(.5)(-.6)(.5) = -.15$. Now if the covariance between $G_w$ and the remainder of the calf's environment for weaning weight ($E_w$) is zero the following equation may be written.

$$-.15 = \frac{\text{cov}(G_w, E_t)}{\left[\text{V}(G_w) \text{V}(P_m^i)\right]^{1/2}} \quad (1)$$

The $\text{cov}(G_w, E_t)$ is the covariance between genotype ($G_w$) and total environment ($P_m^i+ E_w$).
Figure 12. Relations between weaning weight ($P_w$) and maternal environment for weaning weight ($P_m'$).
Since \( \frac{V(P_m)}{V(P_w)} = 0.5 \), then, using \( V(P_w) = 3570 \) from the present study, \( \left[ V(P_m) \right]^{1/2} = 42 \). Also, from the present data, \( \left[ V(G_w) \right]^{1/2} = 30 \). Substituting these values in equation (1) gives \( \text{cov}(G_w, E_t) = -188 \). Using the relation \( V(P_w) = V(G_w) + V(E_t) + 2 \text{cov}(G_w, E_t) \) yields

\[
\begin{align*}
V(G_w) & = 900 \\
V(E_t) & = 3046 \\
\text{cov}(G_w, E_t) & = -188.
\end{align*}
\]

The values computed assuming no correlation were

\[
\begin{align*}
V(G) & = 900 \\
V(E) & = 2670.
\end{align*}
\]

Using this new estimate would change the environmental correlation between weaning weight and gain in the first period from \(-0.19\) to \(-0.18\). Of course the environmental variance for gain in the first period might be biased too. The bias in the environmental correlation is small even assuming a rather strong genetic correlation of \(-0.6\).

The computed heritabilities for each trait were shown in Table 8. Heritabilities summarized from the literature for birth weight, weaning weight, post-weaning gain, and final weight are presented in Tables 17 to 20, respectively.

Heritability of \(0.22\) for birth weight is smaller than found by most of the other workers. The average of the values in Table 17, ignoring the fact that they are not all
Table 17. Heritabilities for birth weight reported in the literature

<table>
<thead>
<tr>
<th>Estimate</th>
<th>Method</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>.22</td>
<td>paternal half-sib</td>
<td>Burris and Blunn (1950)</td>
</tr>
<tr>
<td>.11</td>
<td>paternal half-sib</td>
<td>Dawson et al. (1947)</td>
</tr>
<tr>
<td>.45</td>
<td>paternal half-sib</td>
<td>Gregory et al. (1950)</td>
</tr>
<tr>
<td>.53</td>
<td>paternal half-sib</td>
<td>Knapp and Clark (1950)</td>
</tr>
<tr>
<td>.23</td>
<td>paternal half-sib</td>
<td>Knapp and Nordskog (1946)</td>
</tr>
<tr>
<td>.42</td>
<td>b_{os}</td>
<td>Knapp and Nordskog (1946)</td>
</tr>
<tr>
<td>.34</td>
<td>b_{os/y}</td>
<td>Knapp and Nordskog (1946)</td>
</tr>
<tr>
<td>.35</td>
<td>paternal half-sib</td>
<td>Koch and Clark (1955b)</td>
</tr>
<tr>
<td>.44</td>
<td>b_{od}</td>
<td>Koch and Clark (1955c)</td>
</tr>
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<td>.35</td>
<td>b_{os}</td>
<td>Koch and Clark (1955c)</td>
</tr>
<tr>
<td>.59</td>
<td>paternal half-sib</td>
<td>Shelby et al. (1957)</td>
</tr>
<tr>
<td>.72</td>
<td>paternal half-sib</td>
<td>Shelby et al. (1955)</td>
</tr>
</tbody>
</table>

The wide range of the heritabilities indicate they are subject to large sampling errors and perhaps, in some cases, to biases. Heritability is not, however, a parameter that is invariate for all populations.

The .25 for heritability of weaning weight computed from the present data agrees closely with the average of the values in Table 18.
Table 18. Heritabilities for weaning weight reported in the literature

<table>
<thead>
<tr>
<th>Estimate</th>
<th>Method</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
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<td>.08</td>
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</tr>
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<td>Carter and Kincaid (1959a)</td>
</tr>
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<td>.26</td>
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<td>Gregory et al. (1950)</td>
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<td>.12</td>
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<td>Knapp and Nordskog (1946)</td>
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<td>.30</td>
<td>(b_{os/y})</td>
<td>Knapp and Nordskog (1946)</td>
</tr>
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<td>.24</td>
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<td>Koch and Clark (1955b)</td>
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<tr>
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<td>Koch and Clark (1955c)</td>
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<tr>
<td>.25</td>
<td>(b_{os})</td>
<td>Koch and Clark (1955c)</td>
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<td>paternal half-sib</td>
<td>Rollins and Wagnon (1956)</td>
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<tr>
<td>.23</td>
<td>paternal half-sib</td>
<td>Shelby et al. (1955)</td>
</tr>
</tbody>
</table>

The only heritabilities for gain in successive periods of a feedlot test found in the literature were those of Knapp and Clark (1947). In their data heritability increased for the three successive 84-day periods (.10, .54, and .84). In the present data heritability was largest for the second period and then decreased throughout the remainder of the test. The values of heritability for the five periods were
Table 19. Heritabilities for post-weaning gain reported in the literature

<table>
<thead>
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<th>Method</th>
<th>Reference</th>
</tr>
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<td>.38</td>
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<td>Carter and Kincaid (1959a)</td>
</tr>
<tr>
<td>.54</td>
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<td>Carter and Kincaid (1959a)</td>
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<tr>
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<td>Carter and Kincaid (1959a)</td>
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<td>$b_{os}$</td>
<td>Carter and Kincaid (1959a)</td>
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<td>$b_{od}$</td>
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<td>.57</td>
<td>$b_{od}$</td>
<td>Carter and Kincaid (1959a)</td>
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<tr>
<td>.3 - .5</td>
<td>sel. high and low</td>
<td>Kincaid and Carter (1958)</td>
</tr>
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<td>paternal half-sib</td>
<td>Knapp and Clark (1950)</td>
</tr>
<tr>
<td>.69</td>
<td>paternal half-sib</td>
<td>Knapp and Clark (1951)</td>
</tr>
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<td>.99</td>
<td>paternal half-sib</td>
<td>Knapp and Nordskog (1946)</td>
</tr>
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<td>.46</td>
<td>$b_{os}$</td>
<td>Knapp and Nordskog (1946)</td>
</tr>
<tr>
<td>.97</td>
<td>$b_{os/y}$</td>
<td>Knapp and Nordskog (1946)</td>
</tr>
<tr>
<td>.39</td>
<td>paternal half-sib</td>
<td>Koch and Clark (1955b)</td>
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<tr>
<td>.18</td>
<td>$b_{od}$</td>
<td>Koch and Clark (1955c)</td>
</tr>
<tr>
<td>.46</td>
<td>paternal half-sib</td>
<td>Shelby et al. (1957)</td>
</tr>
<tr>
<td>.60</td>
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<td>Shelby et al. (1955)</td>
</tr>
<tr>
<td>.54</td>
<td>$b_{od}$</td>
<td>Warwick and Cartwright (1955)</td>
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<tr>
<td>.2 - .5</td>
<td>paternal half-sib</td>
<td>Warwick and Cartwright (1955)</td>
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Table 20. Heritabilities for final weight reported in the literature

<table>
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</tr>
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<td>.86</td>
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<td>Knapp and Clark (1950)</td>
</tr>
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<td>.81</td>
<td>paternal half-sib</td>
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<td>.69</td>
<td>$b_{os}$</td>
<td>Knapp and Nordskog (1946)</td>
</tr>
<tr>
<td>.90</td>
<td>$b_{os/y}$</td>
<td>Knapp and Nordskog (1946)</td>
</tr>
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<td>.77</td>
<td>paternal half-sib</td>
<td>Shelby et al. (1957)</td>
</tr>
<tr>
<td>.84</td>
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<td>Shelby et al. (1955)</td>
</tr>
</tbody>
</table>

.18, .28, .18, .08 and .04. This suggests that after the second 28 days on feed, random variations in environment played an increasing role in differences between the calves.

Heritabilities for post-weaning gain range from .18 to .99 in the literature and average about .50. Heritability for total feedlot gain was .40 in this study. Heritabilities of final weight reported in the literature are extremely high, averaging about .8. The value of .47 from this study was much smaller. Only two entirely independent sets of data were represented in Table 20.

Only a few genetic correlations for beef cattle traits appear in the literature. Some of these were presented in the review of literature. Carter and Kincaid (1959) obtained genetic correlations of .66 and .51 for males and females.
between weaning weight and daily gain. The bulls were fed in dry lot while the heifers were on pasture in their study. Koch and Clark (1955b) found the genetic correlations between birth weight and weaning weight, birth weight and daily gain, and weaning weight and daily gain to be .63, .06 and -.03.

The phenotypic, genic and environmental correlations computed in this study were presented in Table 9. In general the genic correlations were quite high, the phenotypic ones were intermediate and the environmental ones were very low or negative. The genic correlations tended to be higher between gains made in adjacent time periods and to be lower as the periods became more remote. Four of the genic correlations were larger than unity. This could have occurred rather easily by chance since the sampling errors were extremely large. No reason is evident for the genic correlations to be biased upward. The genic correlation between weaning weight and gain in the last period was negative. While negative genic correlations are possible, no reason is evident for this correlation to be negative. The genic correlations of birth weight with feedlot gains varied from .12 to 1.03 and oscillated in what seems an illogical manner. The genic correlations of fourth period gain and the other traits were high yet those with fifth period gain were low, despite the high genic correlation between these two periods. If this represents the true situation, it suggests that different genes
begin to express themselves during the fourth period and per­sist for the last 28 days while the genes which were impor­tent before and well into the fourth period cease to affect gain the last 28 days. The genic correlations between wean­ing weight and feed lot gains are large positives. This agrees with Carter and Kincaid (1959) but not with Koch and Clark (1955b). The environmental correlations of weaning weight with the post-weaning gain periods indicated that good pre-weaning environment handicaps a calf early in the test but benefits him later on. This was similar to what was shown by the age of dam constants. Most of the environmental correlations between gain periods were negative. Larger negative values occurred between adjacent periods. Error due to weighing and fill could have contributed to these negative correlations. Every extra pound of fill in an animal at the end of a period automatically makes the gain for that period appear too large and at the same time makes the gain for the next period appear too small. These large negative correlations between adjacent periods also suggest that compensatory gains are a factor.

The indices

The genic and phenotypic parameters were estimated and the indices constructed after the data were corrected for
year, sex, age of dam, and age of calf. The accuracy of the indices depends in part on how perfect were the corrections for these variables. The indices were restricted to linear functions of the $P_i$'s. The present state of knowledge of statistics makes this necessary. This does not imply that linear functions describe gene action more accurately than non-linear ones.

It was assumed that $\text{cov}(G_i, E_j) = 0$ for all $i$ and $j$. The case of $i = j$ was discussed above for weaning weight. These covariances could not be calculated, so their effect on the indices could not be determined.

Since the sampling errors of the information used to construct the indices were high, the indices could be inaccurate. Some of the genic covariances were obviously too high, since some of the genic correlations exceeded unity. No logical way to reduce the size of particular genic covariances and not others was found. If the genic covariances were biased up proportionally, the conclusions based on the indices would not be changed, although the correlations between $G_t$ and $I$ would be too large. That is, the correlations would have indicated accurately the relative amount of information from each index.

The first seven indices in Table 11 considered each trait singly as a predictor of $G_t$. Weaning weight and gain in each of the first two feeding periods contained the most
information about the genic effects for final weight. Gain in the last period contained little information about this, largely because the genic variance for gain in this period and its genic covariance with gains in the other periods were very low.

Adding each trait into an index in the chronological order in which it was expressed increased the correlation, as some information was gained by incorporating each trait. Gain in the last two periods added little information, increasing the correlation only from .80 to .82. Gain in the fourth period gave little additional information despite its high correlation when used alone, because its genic covariances with the other traits were high. The information in this fourth period largely repeated the information which was already in the earlier measures. Gain in the last period increased the correlation only a little because its genic variance was low. This is to be expected if the same genes which affected fourth period gain were already acting earlier and if fifth period gain was influenced largely by non-genetic factors.

Birth weight was a good predictor of the genic effects for final weight. However, a comparison of $I_{16}$ and $I_{11}$ showed that very little information was gained by using birth weight in the index. Selection is not customarily practiced at birth for beef cattle. While birth weight is a good indicator
of the genic effects for final weight, obtaining birth weight added little if the other traits were to become available later. Some cattlemen select their breeding stock at weaning time. If a feeding test is not part of the selection program, including birth weight in the index to predict the genic effects for final weight might be worth while, as the correlation of the index with \( G_t \) increased from .49 to .54 when birth weight was used in conjunction with weaning weight. In some purebred herds, where the calves are tattooed at birth and thus handled anyway, birth weight could be taken with slight additional effort. In this case it should be advantageous to do so. But much more needs to be known concerning other consequences of selecting for heavier calves at birth, such as the possible increase in difficult parturitions.

If a breeder is selling calves at weaning the correlation of the genic effects for weaning weight \( (G_p) \) and an index predicting this would be of interest where \( I_1'' = bP_2 \) and \( I_2'' = b_1P_1 + b_2P_2 \). These indices turn out to be

\[
I_1'' = .25 P_2, \text{ where } r_{G_2I_1''} = .50 \text{ and }
\]

\[
I_2'' = .61 P_1 + .22 P_2, \text{ where } r_{G_2I_2''} = .53.
\]

Hence birth weight seems to add very little information about the genic effects for weaning weight when weaning weight itself is known.

\( I_{13} \), which incorporates all available information, is
little better than $I_{16}$ which omits birth weight and gain in the last 56 days. In this case $I_{16}$ is $0.79/0.82 = 0.96$ as efficient for selection as $I_{13}$. It is worth while to consider how much would be lost by not weighing the calves every 28 days of the feeding test. The index $I_{19} = b_1 P_2 + b_2 (P_3 + P_4 + P_5)$ turns out to be $I_{19} = 0.32 P_2 + 1.15 (P_3 + P_4 + P_5)$, where $r_{0tI_{19}} = 0.78$. Thus the correlation is decreased only from 0.79 to 0.78 by considering total 84-day gain rather than each of the three gain periods separately. Also $I_{19}$ gives $0.79/0.82 = 0.95$ as much information as $I_{13}$ which uses all traits in the most efficient manner.

The correlations between $G_t$ and $I'$ in Table 12 showed that gain in all five periods was only a little more useful in predicting the genic effects for 140-day gain than gain in the first three periods. Gain in the first three periods was $0.68/0.72 = 0.94$ as efficient as gain in all five periods. The genic effects for feedlot gain ($G_t$) would be of primary interest to a feeder who buys calves at weaning.

The conclusion of Knapp and Clark (1947) that the feeding period of 252 days used in their study could not be shortened without serious loss of information is in sharp contrast to the evidence of the present work. While the following is partly speculation, it offers a possible explanation for the discrepancy between the two studies. Their conclusion was determined to a large extent by the fact that
heritability increased in size for their three successive periods (.10, .54 and .84). In their study each sire's progeny were fed together in a pen separate from the other progeny groups. Sire differences, on which the heritabilities were based, were entirely confounded with pen differences. If environment actually becomes more important as the feeding test continues, as the present study indicated, any pen effects which may have existed would have been more important in the later periods. If environmental correlations existed between the periods for the animals in a pen, the pen effects would accumulate, thus increasing the differences between pens. This would have caused an upward bias in the heritabilities calculated for the second and third periods and in the genic correlations.

Morley (1950) gave the increase in each trait per unit of I as \( \sum b_j \text{cov}(G_i, G_j) / V(I) \). For the seven traits these were .06, .55, .14, .14, .09, .07 and .01, respectively. The sum of the last six (omitting birth weight) equals unity since the increase for birth weight is also included in the increase for weaning weight. The expected increase in pre-weaning gain would be .49.

The change in \( G_t \) which can be achieved by selection is proportional to the reach \( (I_g - I_p) \) which is attained. If I is distributed normally and selection is by truncation and entirely on the basis of I then \( (I_g - I_p) = z/b [V(I)]^{1/2} \)
where \( b \) is the fraction saved to be parents and \( z \) is the height of the ordinate of a standard normal curve at the truncation point.

In practice selection could never be entirely on \( I \) since some natural selection would occur. Any deviation from truncation selection on the basis of \( I \), such as paying attention to fancy points or even to important physical defects, decreases \( I_s - I_p \). Though some deviation necessarily will occur, it should be minimized as much as possible.

For the index \( I_{19} = 0.32 P_2 + 1.15 (P_3 + P_4 + P_5) \) the standard deviation was 43. This index was computed for each of the 748 calves for which the required traits were available. The average index was 238.3. This value appears low because the traits were all adjusted down by subtracting the constants for the environmental variables. This occurred merely because the lowest level of a classification (e.g., heifers and two-year-old cows) were set equal to zero to solve the least squares equations. This is of no consequence, since the indices may be coded up or down without changing the order of the animals.

If some selection could be practiced at weaning considerable saving in cost would result from feeding fewer calves. It would be desirable to cull some calves on weaning weight if this could be done without decreasing seriously the progress from selection. Culling on weaning weight would de-
crease gain from selection by decreasing the reach \((I_{g} - I_{p})\) which could be practiced at the end of the feeding test. The situation is presented geometrically in Figure 13. When some animals are culled on weaning weight \((P_{g})\), \(x\) are culled which would have been saved if selection had been for \(I\) alone. Since \(w + x\) animals are needed for breeding stock, the culling level for \(I\) must be enough lower so that \(w = x\). The size of \(x\) depends on the cost of the feeding test and the economic value of a unit of the index.

The problem of what fraction might be culled at weaning was examined empirically, using the 748 animals for which \(I_{15}\) could be computed. Table 21 shows the results of this study. The reach in terms of units of \(I\) is shown for various fractions of the population of calves following culling at several different levels on weaning weight. In every case the fraction is based on the entire 748 calves. Most any situation may be examined in the table. For example, a breeder maintaining his herd size and not selling breeding stock might need to save 10 percent of the bulls and 40 percent of the heifers. Mr. Haigler, on the other hand, saves about 60 percent of the heifers and 30 percent of the bulls either to use as replacement stock or to sell as breeding stock.

To illustrate the use of Table 21 suppose that .4 of the calves weaned must be saved as breeding stock. Locate .4 on the left margin of the table. Then, if the heaviest .8
Figure 13. Effect of early culling, solely for weaning weight ($P_2$), on selection for the index ($I_{19}$)
\[ r_{P_2I} = 0.64 \]
\[ \sigma_I = 43 \]
\[ \sigma_{P_2} = 60 \]
Table 21. Empirical reach in $I_{19}$ for various fractions saved for different levels of culling on weaning weight

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*a* Fraction of calves at weaning selected on weaning weight.

*b* Fraction of calves at weaning selected for $I$ after the 84-day gain test.

*c* $I_S - I_p$ where $I_p = 238.3$.

of the calves at weaning were placed on the feeding test, the reach in units of the index would be 39.6. If only .6 were placed on the feeding test the reach would be 37.5.

Just as, for a given correlation between $I$ and $P_2$, the optimum size of area $x$ in Figure 13 depends on the value of a unit of $I$ and the cost of feeding a calf 84 days, the amount of reach one is willing to sacrifice in order to cull
a certain fraction at weaning depends on these two things. The values in Table 21 indicate that some advantage could be taken of the high correlation between $F_2$ and $I$ by culling some calves at weaning. The loss in reach for $I$ might be small compared to the saving in early disposal of many calves, most of which would be culled eventually anyhow.

Table 22 contains the theoretical reach in $I$ that can be practiced after culling on weaning weight. It compares closely with the actual values, shown in Table 21, for these 748 calves. These theoretical values were computed as the product of $z/b$ and the variance remaining in $I$ after selection for weaning weight. As before, $b$ is the fraction saved on the basis of $I$ and $z$ is the height of the ordinate at the truncation point.

The reduced variance in $I$ was computed by the following formula given by Cochran (1951):

$$V(I) \left( 1 - \frac{r^2}{F_2} I \frac{z(z - t)}{a} \right)$$

In this formula $t$ is the abscissa and $z$ is the ordinate of a standard normal distribution when the fraction $a$ is truncated on weaning weight. Computing the theoretical reach as $z/b$ times the remaining variance in $I$ assumed the distribution of $I$ was normal after some culling for weaning weight. This, of course, is not true and is the primary reason why the theoretical values exceeded the empirical ones, especially
Table 22. Theoretical reach in $I_{19}$ for various fractions saved for different levels of culling on weaning weight

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$^a$Fraction of calves at weaning selected on weaning weight.

$^b$Fraction of calves at weaning selected for $I$ after the 84-day gain test.

$c_{z/b} V(I) \left[ 1 - r_{P2}^2 \frac{2}{a} s (z - t) \right]$ where $t$ is the abscissa and $z$ is the ordinate at the point of truncation.

when the fraction saved was near one or zero.

Since the empirical values were obtained by sampling a finite population, they were subject to sampling error. Also the theoretical and empirical values might have differed because $I$ may not have been distributed quite normally before
selection. The nature of the errors, free of the complication of skewedness of the distribution of I resulting from selection on weaning weight, can be seen by comparing theoretical and empirical reach when no selection was practiced for weaning weight. These values were in fairly close agreement. According to Dickerson and Hazel (1944), the skewedness resulting from culling on P_2 would not be an important factor even when r_{P_2I} is as large as .8 unless the fraction saved is near one or zero.
SUMMARY

The primary objective of this analysis was to determine the length of the feeding test necessary for the accurate selection of beef cattle for their genetic ability to gain weight. The traits studied were birth weight, weaning weight, and gain in each of five successive 28-day feeding periods, for purebred Hereford calves in an Ohio herd. Information was available on 832 calves over nine years.

The interactions among the environmental variables year, sex, age of dam and age of calf at weaning were examined. The interaction between age of calf and sex was important, as was anticipated. The interaction between age of dam and year was surprisingly large. This could have been due to confounding of sires with age of dam - year subgroups, confounding of first and second calf three-year-old cows with years, or a true interaction between these variables. Least squares constants for the important environmental effects were computed and were used to correct the data.

Estimates of the phenotypic, genic and environmental variances and covariances were computed from paternal half-sib analyses of variance and covariance of the corrected data. These were used to compute heritability for each trait and the phenotypic, genic and environmental correlations among the seven traits. The heritabilities were generally lower than those reported in the literature. The genic correlations
were quite high, the phenotypic correlations were intermediate and the environmental correlations were low or negative.

Several selection indices were computed, using various combinations of the traits. Indices were computed to predict the sum of the average effects of the genes which influence final weight at about one year of age, 140-day feedlot gain and weaning weight. Though birth weight was a good indicator of the genic effects for these characteristics, it was of little additional value if later weights were taken. Since selection is not customarily practiced at birth for beef cattle, it does not seem worth while to record birth weight. If feedlot gains were not available and birth weight was easily obtained, it might be worth while to include it in an index predicting final weight.

Gain in the last two feeding periods added little information about the genic effects for either final weight or post-weaning gain. Since the cost of feeding the calves an additional 56 days would be considerable, the feeding period could be shortened to 84 days with almost no loss of genetic information. An index including weaning weight and total gain in the 84-day period was .99 as efficient for selecting for final weight as one with weaning weight and gain in each of the three 28-day periods considered separately.

The index which was most desirable, when selecting for final weight, considering the gain expected from selection and
the cost involved, was

\[ I = 0.32(\text{weaning weight}) + 1.15(84\text{-day gain}) \]

or, for convenience,

\[ I = 0.28(\text{weaning weight}) + (84\text{-day gain}). \]

This index was .95 as efficient as one combining all traits in the most efficient way. Before use in the index, the weights should, of course, be corrected for those environmental variables for which the data in this study were corrected.

Practical considerations might alter the choice of index. For example, if a breeder wants to feed his cattle longer than 84 days to fatten them for sale either as breeding stock or as market cattle, he should utilize the slight additional information furnished by the gain made after 84 days. It would be desirable to know what loss in accuracy would result from selection based on pasture gains. This alternative would be especially useful for selecting replacement heifers.

Since the correlation between weaning weight and the index was high (.64), some culling at weaning could be done. How much would depend on the fraction to be saved, the cost of the feedlot test and value of a unit of the index. How much less reach for the index could be practiced, if some had been culled at weaning, was examined empirically, using the calves in this study, for various levels of culling at weaning and different fractions saved at the end of the test. The
results suggested that at least 30 percent of the bulls could be culled at weaning, without a serious decrease in reach, if 30 percent were to be saved, and at least 10 percent of the heifers could be culled if 60 percent were to be saved.

If the conclusions suggested by this study are valid, *viz.* that a short feedlot test is adequate for selection for weight and that a moderate amount of culling may be done at weaning, beef cattle breeders should be encouraged to undertake a testing program of this type.
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