ANALYSES of genetic variation in beef cattle have indicated that selection for rapid growth rate should improve efficiency of gain because of the high heritability of gain (Gregory, 1969) and its favorable associations with feed conversion (Koch et al., 1963; Swiger et al., 1962; Swiger et al., 1965) and value of retail product above feed cost (Swiger et al., 1965). Differences in final weight account for 80 to 88% of the variation in weight of boneless retail trimmed beef on an age constant basis (Cundiff and Gregory, 1968).

The purpose of this study was to evaluate the expected effect of selection for growth rate on composition and quality of beef carcasses and to further evaluate the genetic relationships among various indicators of carcass quality and composition and yields of retail product, fat trim and bone.

Materials and Methods

The data were obtained on 503 steers in 75 sire progeny groups produced from 1961 through 1965 in the heterosis experiment involving Angus, Herefords and Shorthorns at the Fort Robinson Beef Cattle Research Station. The design of Phase I and Phase II of this experiment and the distribution of progeny by breeding group are presented in an earlier report (Cundiff et al., 1969). The feeding and management and carcass cut-out procedures used in obtaining retail product, fat trim and bone have been presented by Gregory et al. (1965, 1966a, b).

In this study carcass weight adjusted for age was used as the measure of growth rate. A U.S.D.A. grader evaluated carcasses for marbling to the nearest one-third of a degree (e.g., slight—, slight, slight+).

Fat thickness was measured on tracings of the 12th rib at a distance three-fourths of the way across the long axis from the medial end of the l. dorsi muscle. The l. dorsi area was also measured from these tracings and the estimate of carcass cutability (percent of closely trimmed-boneless retail cuts from the round, loin, rib and chuck) was derived from the equation presented by Murphy et al. (1960) involving a single measure of fat thickness, percent kidney fat (estimated by a U.S.D.A. grader), l. dorsi area and carcass weight.

Estimated cutability was included for comparison with actual weight of closely trimmed-boneless retail product in the primal cuts (round, loin, rib and chuck) adjusted for carcass weight, since Dinkel et al. (1965) found the latter to be a more desirable method of evaluating variation in proportion of retail product.

Three analyses were made. (1) Regression adjustment for age at slaughter was used to estimate variation and covariation for rate and composition of growth and indicators of carcass composition and quality. (2) Regression adjustment for carcass weight was used to examine variation in proportions of retail product, fat trim and bone and associations with indicators of carcass composition and quality. In this analysis, much of the genetic variation in growth rate is removed. (3) Regression adjustment for both age and carcass weight was used to examine variation in differential growth of lean, bone and fat. The analyses and procedures followed in estimating genetic, environmental and phenotypic parameters were described in an earlier report (Cundiff et al., 1969).

Results and Discussion

Heritabilities. The estimates of heritability, phenotypic standard deviations, coefficients of variation and least squares means for traits considered in this study are presented in table 1.
The estimated heritability of carcass weight adjusted for age (0.56) is in general agreement with most estimates for postweaning growth rate and yearling weight in earlier studies (Gregory, 1969). The heritabilities for marbling (0.31, 0.33 and 0.30), fat thickness (0.50, 0.53 and 0.51), l. dorsi area (0.41, 0.32 and 0.32) are similar to the average of estimates in previous reports (Knapp and Nordskog, 1946; Knapp and Clark, 1950; Dawson, Yao and Cook, 1955; Shelby et al., 1962; Christians et al., 1962; Shelby et al., 1963; Cundiff et al., 1964; Busch, 1968). The heritability of l. dorsi area was lower when carcass weight was held constant (0.32) than when age was held constant (0.41) because the genetic correlation between carcass weight and l. dorsi area was higher than the environmental correlation (table 2) in these data.

The heritability of estimated cutability adjusted for age (0.28) was slightly lower than the 0.40 reported by Cundiff et al. (1964) and the 0.66 reported by Busch (1968). The heritability for estimated cutability was slightly higher (0.35) when carcass weight was held constant because the association between cutability and carcass weight was more largely environmental than genetic (table 2).

**Correlations of Growth Rate with Carcass Quality and Composition.** The genetic, environmental and phenotypic correlations of carcass weight with various indicators of carcass quality and composition and with retail prod-

<table>
<thead>
<tr>
<th>Trait</th>
<th>Carcass weight, kg</th>
<th>Marbling</th>
<th>Fat thickness</th>
<th>L. dorsi area</th>
<th>Cutability estimate</th>
<th>Retail product from round</th>
<th>Retail product from primal cuts</th>
<th>Fat trim from primal cuts</th>
<th>Retail product from carcass</th>
<th>Fat trim from carcass</th>
<th>Bone from carcass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.56±.01</td>
<td>0.23</td>
<td>0.34</td>
<td>0.66</td>
<td>0.41±.17</td>
<td>0.93±.05</td>
<td>0.95±.03</td>
<td>0.78±.13</td>
<td>0.94±.03</td>
<td>0.80±.11</td>
<td>0.86±.09</td>
</tr>
<tr>
<td></td>
<td>0.33±.01</td>
<td>0.14</td>
<td>0.43</td>
<td>0.39</td>
<td>0.28±.17</td>
<td>0.77±.05</td>
<td>0.85±.03</td>
<td>0.72±.13</td>
<td>0.86±.03</td>
<td>0.72±.11</td>
<td>0.74±.09</td>
</tr>
<tr>
<td></td>
<td>0.35±.01</td>
<td>0.17</td>
<td>0.38</td>
<td>0.52</td>
<td>0.25±.17</td>
<td>0.86±.05</td>
<td>0.91±.03</td>
<td>0.73±.13</td>
<td>0.91±.03</td>
<td>0.75±.11</td>
<td>0.78±.09</td>
</tr>
</tbody>
</table>

* Standard errors for genetic correlations.
uct, fat trim and bone are presented in table 2. All variables were adjusted for differences in age at slaughter.

The genetic correlation between carcass weight and marbling was low but positive (0.23 ± 0.31). This is higher than comparable estimates between final live weight and grade of —.14 reported by Swiger et al. (1965) and —.28 reported by Busch (1968), but similar to 0.24 reported by Shelby et al. (1963) for carcass weight and grade and slightly lower than 0.47 reported by Cundiff et al. (1964) between carcass weight per day of age and grade.

The high positive genetic correlation estimated between l. dorsi area and carcass weight adjusted for age (0.66 ± 0.19) is higher than 0.15 between carcass weight and l. dorsi area reported by Shelby et al. (1963) but in exact agreement with 0.66 between carcass weight per day of age and l. dorsi area reported by Cundiff et al. (1964) and similar to the estimate of 0.54 between final weight adjusted for age and l. dorsi area reported by Busch (1968).

The low negative estimate for the genetic correlation adjusted for age between carcass weight and estimated cutability (—.33 ± .29) is comparable to that of —.25 between final weight adjusted for age and actual percent retail product reported by Swiger et al. (1965) and is within sampling error of the genetic correlation of 0.02 between carcass weight per day of age and estimated cutability reported by Cundiff et al. (1964). However, Busch (1968) has reported a genetic correlation of 0.74 between estimated cutability and final weight adjusted for age.

Direct and correlated responses from a selection differential of one standard deviation for carcass weight adjusted for age (table 3) were computed to evaluate the expected effects of selection for growth rate on carcass composition and various indicators of carcass composition and quality in terms comparable to those previously reported for selection based on growth and proportion of retail product in the carcass (tables 10, 11; Cundiff et al., 1969).

The data in table 3 indicate that one generation of selection for carcass weight adjusted for age would be expected to increase fat trim more (3.72 vs. 2.74 kg) but retail product and bone less (8.44 vs. 9.57 and 1.22 vs. 1.48 kg) compared with selection for age adjusted weight of retail product (table 10, Cundiff et al., 1969). Thus, if slaughter age was standardized and animals were carried to heavier average carcass weight in the succeeding generation, percent fat trim would rise about 0.58, percent bone would decline about 0.34 and percent retail product would decrease only 0.23. After several generations such changes would become noticeable and impor-

### TABLE 3. EXPECTED DIRECT RESPONSE FOR GROWTH (CARCASS WEIGHT ADJUSTED FOR AGE) AND CORRELATED RESPONSE IN CARCASS COMPOSITION AND QUALITY

<table>
<thead>
<tr>
<th>Trait</th>
<th>Generation 0</th>
<th>Generation 1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ya</td>
<td>Ya + ΔG</td>
</tr>
<tr>
<td>Carcass weight, kg</td>
<td>227.9</td>
<td>13.0</td>
</tr>
<tr>
<td>Retail product—carcass, kg</td>
<td>153.3</td>
<td>8.4</td>
</tr>
<tr>
<td>Fat trim—carcass, kg</td>
<td>39.8</td>
<td>3.7</td>
</tr>
<tr>
<td>Bone—carcass, kg</td>
<td>34.7</td>
<td>1.2</td>
</tr>
<tr>
<td>L. dorsi area, cm</td>
<td>69.0</td>
<td>1.9</td>
</tr>
<tr>
<td>Fat thickness, cm</td>
<td>1.10</td>
<td>0.07</td>
</tr>
<tr>
<td>Cutability estimate,*</td>
<td>50.2</td>
<td>—.2</td>
</tr>
<tr>
<td>Marbling</td>
<td>5.5</td>
<td>0.2</td>
</tr>
</tbody>
</table>

*Ya is the mean for each trait in the present study.

ΔG is the predicted genetic change. Direct response was computed as h²σp and correlated as h₂, hₚ, σpₑ, σₚₑ where h₂ and σₚₑ are the heritability and phenotypic standard deviation of the trait selected, hₚ and σₚₑ are the square root of heritability and phenotypic standard deviation of the unselected trait and rₑₑ is the genetic correlation.

Ya + ΔG is the predicted mean after one generation of selection.

Ya + ΔG - B.Xa is the predicted mean after one generation of selection if average carcass weight is standardized (by slaughtering at a younger age). The partial regression coefficients on days of age at slaughter (Bᵪ) were 0.40 ± .06 for carcass weight (kilograms per day), 0.22 ± .04 for retail product, 0.11 ± .02 for fat trim and 0.05 ± .01 for bone in the carcass while those for l. dorsi area, fat thickness, cutability and marbling were 0.08 ± .03 cm/day, 0.0074 ± .002 cm/day, —.005 ± .007%/day and 0.018 ± .014 units/day, respectively.

* Cutability estimate=52.56—4.95 (single fat thickness, in.), —1.06 (kidney fat, %), +0.682 (rib-eye area, sq. in), —.008 (carcass wt. lb).

Marbling: 5=small—, 6=small+, 7=small++, 8=modest—, etc.
tant. However, if average carcass weight is maintained unchanged by slaughtering at younger ages, expected change in carcass composition is slight and in a desirable direction (+.26\% in retail product, —.07\% in fat trim and —.18\% in bone).

Selection for growth rate can be more intense and implemented at less cost based on yearling weight of live animals than direct selection for carcass retail product. Also, selection for proportion of retail product is expected to produce only about \( \frac{1}{2} \) as much genetic increase in retail product at a given age (2.64 kg vs. 8.44 kg, table 11, Cundiff et al., 1969, and table 3).

Selection differentials of one standard deviation for carcass weight or for proportion of retail product seem optimistic, even if selection were among bulls whose semen was collected and frozen prior to slaughter and especially if selection were based on data for progeny or collateral relatives. On the other hand, a selection differential of 1.5 standard deviations (\( 2\sigma \) in males and \( 1\sigma \) in females) can be achieved for yearling weight and the genetic correlation between carcass weight adjusted for age and yearling weight should be nearly 1.0. Thus, the effect of selection for yearling weight on proportion retail product, fat trim and bone should be even more comparable than the results assuming equal selection intensity would indicate. This does not take into account the other advantages of selecting for yearling weight on economy of production discussed by Koch et al. (1963) and Swiger et al. (1965). Swiger et al. (1965) have demonstrated that use of live animal indicators of fatness in conjunction with yearling weight, to select for retail product growth, could improve the effect on carcass composition without reducing the response on efficiency of retail product growth.

The effect of selection for carcass weight adjusted for age on indicators of carcass composition and quality are also given in table 3. If age at slaughter were standardized and the cattle in the subsequent generation were carried to a heavier average carcass weight, these results indicate that selection for growth would increase \( l.\ dorsi \) area, increase fat thickness slightly, reduce estimated cutability slightly, and increase marbling slightly. If the subsequent generation was slaughtered at a younger age to maintain the same average carcass weight, the \( l.\ dorsi \) area and fat thickness would be essentially unchanged, while carcass cutability would be improved slightly and marbling score would be reduced only .12 of a degree (e.g., one degree = small to modest).

It can be hypothesized that muscle and bone growth have positive associations with mature size, while higher rates of fat deposition and marbling are associated with earlier maturity and negatively associated with mature size. The low positive genetic correlation between carcass growth and marbling suggests that there are some genes affecting both traits in the same direction but others with independent or opposite effects on the two traits. If selection can increase the frequency of genes with positive effects on both traits it may be possible to alter the shape of the growth curve by increasing early growth relative to mature size.

Correlations between Composition and Quality. Genetic, environmental and phenotypic correlations among marbling; estimated cutability; and yields of retail product, fat trim and bone in the primal cuts and carcass from the age constant and weight constant analysis are given in table 4. Estimates from the analysis including both age and weight as covariates are not tabulated because they were so similar to those from the analysis where weight was the single covariate.

Estimates from the age constant analysis indicate that marbling has a low genetic association with growth of retail product and bone in the primal cuts and the carcass. However, rate of fat deposition has a very high positive genetic correlation with marbling.

Estimates from the weight constant analysis indicate that genes influencing marbling have a large positive influence on proportion of fat trim and a sizeable negative influence on proportion retail product and bone in the carcass.

These results agree with findings of Cundiff et al. (1964) and Swiger et al. (1965) who also reported large negative genetic correlations between cutability and carcass grade (—.80) and between percent retail product and carcass quality grade (—.85), respectively. Busch (1968) reported lower genetic correlations between edible portion adjusted for weight and carcass grade adjusted for age and weight (—.38) and marbling adjusted for age and weight (0.02).

The high genetic correlations between estimated cutability and proportion of retail product in the primal cuts or carcass (i.e., weight constant) indicates that selection for estimated cutability would be effective in im-
proving actual proportion of retail product in
the primal cuts and in the carcass. However,
such selection clearly would lead to reduced
marbling and carcass grade. The high nega-
tive genetic correlations between marbling
and proportion retail product (or cutability)
obtained in this study would make index se-
clection for these traits ineffectual unless the
relative economic importance of one was con-
sidered much greater than the other. In that
case the most important trait would be im-
proved while the other was reduced.

These results indicate that selection for
growth rate (table 3) is the best alternative,
since it would improve efficiency of production
(Swiger et al., 1962; Koch et al., 1963;
Swiger et al., 1965) and be accompanied by
gradual changes in carcass composition and
quality, the extent and direction of which
could be controlled by the weight or age of the
animals at slaughter. This is especially true if
nutritional and management programs can be
developed to control marbling and external
fat deposition. The low environmental corre-
lations between marbling and fat trim found
in this study suggest that fat trim found
effects on these control may be feasible.

Summary

Data were obtained on 503 steers in 75 sire
progeny groups from a heterosis experiment
involving Angus, Herefords and Shorthorns.
Analysis of genetic variation within breed
and sire breed of dam groups indicated that
selection for rate of growth would be effective
and that associated changes in carcass com-
position and marbling would be greatly in-
fluenced by age or weight at slaughter. If
slaughter age were standardized from one gen-
eration to the next, carcass weight and quant-
ity of retail product, fat trim and bone would
be increased, marbling and bone would be reduced; if slaughter age were maintained unchanged, weight of animals at slaughter would be increased, marbling score and % retail product would be improved, slightly while % bone would be reduced. If weight of animals at slaughter were maintained constant then % retail product would be improved slightly while % fat trim, % bone and marbling score would be reduced slightly.

A low positive genetic correlation was found
between growth rate and marbling, suggesting
that if muscle and bone growth are positively
and if marbling and fatness are negatively
associated with mature size and age, mar-
ning and growth rate would be improved.

TABLE 4. GENETIC (G), ENVIRONMENTAL (E) AND PHENOTYPIC (P) CORRELATIONS AMONG MEASURES OF CARCASS COMPOSITION AND QUALITY

<table>
<thead>
<tr>
<th>Estimated cutability</th>
<th>Primal cuts</th>
<th>Carcass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Retail product</td>
<td>Fat trim</td>
</tr>
<tr>
<td>Age constant</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marbling</td>
<td>G</td>
<td>-1.22±.31*</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>-0.33</td>
</tr>
<tr>
<td>Estimated</td>
<td>G</td>
<td>-0.84±.33</td>
</tr>
<tr>
<td>cutability</td>
<td>E</td>
<td>-0.23</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>-0.16</td>
</tr>
</tbody>
</table>

Carcass weight constant

| Marbling             | G           | -1.13±.27 | -1.08±.25 | 1.10±.25 | -0.85±.29 | -0.89±.22 | 0.98±.22 | -0.78±.46 |
|                      | E           | 0.16      | 0.04     | 0.09     | -0.07     | -0.06     | 0.08     | -0.03     |
|                      | P           | -0.28     | -0.38    | 0.41     | -0.31     | -0.37     | 0.40     | -0.20     |
| Estimated            | G           | 0.86±.16  | -1.00±.15 | 0.80±.26 | 0.80±.16  | -1.03±.14 | 0.89±.41 | -0.03     |
| cutability           | E           | 0.52      | -0.43   | 0.18     | 0.54     | -0.38     | 0.11     | 0.29      |
|                      | P           | 0.63      | -0.62   | 0.38     | 0.64     | -0.61     | 0.29      | 0.29      |

* Standard errors for genetic correlations.
ture size, then it may be possible to alter the shape of the growth curve through simultaneous selection for marbling and growth rate.

Genetic correlation of marbling score was highly positive with fat trim and mildly negative with weight of retail product and bone at constant age and was highly positive with fat trim and strongly negative with yield of retail product and bone at a constant carcass weight. This indicated that maintaining marbling would not be compatible with reducing fat trim at a constant age or weight or with increasing yield of retail product at a constant carcass weight. Primary opportunity for genetic improvement by selection seems to be in more rapid and efficient growth rate rather than in higher proportion of retail product. However, a low environmental correlation between marbling score and weight of fat trim suggests that marbling score may be controllable through nutritional management independent of fat deposition contributing to fat trim.

Literature Cited


