This bulletin is dedicated to Dr. R. T. Clark, who was coordinator of the beef cattle breeding research program in the Western Region, and to J. R. Quesenberry, who was Superintendent of the U.S. Range Livestock Station, Miles City, Montana, for many years. These men were pioneers in beef cattle breeding research.

Shown in the picture above are Dr. Clark (right) and Mr. Quesenberry (left) taking records on some cattle.
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COOPERATING AGENCIES: The Agricultural Experiment Stations of Arizona, California, Colorado, Hawaii, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming; the Cooperative State Research Service, United States Department of Agriculture; and the Agricultural Research Service, United States Department of Agriculture.

Under the procedure of cooperative publications, this regional bulletin becomes, in effect, an identical publication of each of the cooperating agencies, and is mailed under the frank and indicia of each. Supplies of this publication are available at the sources listed above. It is suggested that requests be sent to one source only.
Cooperative research on beef cattle breeding in the western region has resulted in the development of much knowledge during the past 25 years. Subsequent to the passage of the Research and Marketing Act in 1946, a means was provided for organizing cooperative research on a relatively large scale. Regional research projects on beef cattle breeding were initiated in the Western, Southern, and North Central regions. The regional project in the Western Region (Project W-1) had as its original objectives:

1. To develop inbred lines of beef cattle that will be useful in the improvement of such characters as rate of gain, economy of gain, carcass quality, fertility, and longevity.

2. To develop effective breeding techniques for improving the productiveness of beef cattle.

3. To investigate the productivity of existing lines of beef cattle.

The original project was revised in 1956 with new objectives as follows:

1. To develop lines of established beef cattle breeds that will be useful in the improvement of economically important characteristics such as weaning, weight, rate of gain, economy of gain, carcass composition, fertility, and longevity.

2. To develop selection criteria and selection and breeding techniques which will be effective in the derivation of productive lines of beef cattle.

3. To study the inheritance of specific genes and factor interactions.

4. To determine the genetic causes of decline in vigor, size, fertility, and other characteristics of inbred lines that have been or may be established.

5. To study the adaptation of lines of beef cattle of known genetic merit to new environments.

6. To introduce and test new or derived breeds or types of cattle.

Project W-1 was terminated in 1970 by action of the Western Regional Experiment Station Directors, but Western Regional Coordinating...
Committee 1 was established to give investigators working cooperatively on beef cattle breeding research an opportunity to prepare some of the remaining research material for publication. One of the publications the WRCC-1 Committee considered was a summary of beef cattle breeding research in the Western Region.

The members of the W-1 and the WRCC-1 Committees express their sincere appreciation to the Directors of the Agricultural Experiment Stations of the Western Region and to the Agricultural Research Service of the USDA for their help in this team approach to research.

INTRODUCTION

This bulletin has been prepared to provide a summary of beef cattle breeding research in the Western Region for the beef cattle industry and for other scientists working in beef cattle breeding and related research. It contains highlights of research done prior to 1963, which was reported in Oregon Agricultural Experiment Station Technical Bulletin 73, a Western Regional publication, and a more complete summary of research accomplishments following 1963. It is not the intent in this publication to report details of any of the research but rather to summarize (1) what has been done, (2) the principles, concepts, and methodologies that have been developed, and (3) the significance of the research to the livestock industry.

The order of presentation was developed primarily on the basis of the reader getting the most information rather than on the basis of when or where the research was done. Major publications are listed in the literature cited section but abstracts, theses, leaflets, and trade journal articles have been omitted unless they contain particularly important items because many of these publications are difficult to locate.

FACTORS AFFECTING PRODUCTION TRAITS

The five most important production traits in beef cattle are reproductive ability, preweaning gains, postweaning rate of gain, feed conversion efficiency, and ability of the animal to produce a desirable carcass. Birth weight is also important because very small calves may fail to survive, extremely large calves at birth may cause calving problems, and size at birth may influence subsequent rates of gain. The heritabilities of production traits are presented in Table 1. Birth weight, postweaning rate of gain, yearling weight, final feedlot weight, mature size, feed efficiency, and yearling grade are generally highly heritable (0.30 and higher), while suckling gains are lowly to moderately heritable (under 0.30).

Heritability estimates and repeatability of reproductive performance (measured as calving percentage, services per conception, or calving...
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<td>.10 (1st 84 days)</td>
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<td>.92</td>
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<td>.48, -.35</td>
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<td>.36</td>
<td>Marchello et al., 1960</td>
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<td></td>
<td>.10 (steers)</td>
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<tr>
<td></td>
<td>.71 (heiifers)</td>
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Table 1. Heritability Estimates for Production Traits—(Continued)

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<td></td>
<td>.48</td>
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<td>.34 (heifers)</td>
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1 Heritabilities of 0 to 0.15 are low, from .15 to .35 are intermediate, and above .35 are high.
difficulty) are low. Davenport and others (1965) gave 0.15 and 0.14 as estimates of heritability in inbreds and linecrosses, respectively. Heritability and repeatability of calving interval is zero (Brown et al., 1954). Heritability of calving difficulty as a trait of the calf was found to be 0.07 for all calvings and 0.13 for two-year-old cattle, while calving difficulty as a trait of the dam was 0.13 for all calvings and -.003 for two-year-old cows (Brinks, Olson, and Carroll, 1973). Calving difficulty is important economically as shown by fewer calves weaned per cow exposed and lighter weights in calves from three-year-old cows that had calving problems at two years of age. Lesmeister, Burfening, and Blackwell (1973) noted that heifers that calved early had a slight tendency to calve early throughout their productive lives, but the repeatability of time of calving is low. Early calving heifers tended to be more productive than heifers calving late.

Mature cows (Sawyer et al., 1949; Koch and Clark, 1955a) and larger cows of comparable ages (Koch and Clark, 1955a,b,c,d) produce larger calves at birth than younger cows and smaller cows. Male calves are generally larger at birth than females (Koch and Clark, 1955a; Flower et al., 1963; Kress and Burfening, 1972).

Preweaning gains or weaning weights of calves adjusted to a common age are larger from mature cows than from younger cows, and larger cows of comparable ages wean heavier calves than smaller cows (Sawyer et al., 1948; Rollins and Guilbert, 1954; Koch and Clark, 1955a; Nelms and Bogart, 1956; Blackwell et al., 1958; Pahnish et al., 1958; Brinks et al., 1964b; Linton et al., 1968; Mahmud and Cobb, 1963; Flower et al., 1963; Kress and Burfening, 1972). Year effects have been found in all studies, indicating that feed conditions affect preweaning gains. Heavier calves at birth and calves born within a year or season of the year that permits the nursing cow to be under better pasture conditions reach heavier weaning weights (Rollins and Guilbert, 1954; Koch and Clark, 1955b; Bogart et al., 1956; Nelms and Bogart, 1956; Clark et al., 1958).

Weaning weights are important economically (Lindholm and Stonaker, 1957) and must be included in a selection program; however, there may be a negative genetic correlation between milk production and postweaning rate of gain (Koch and Clark, 1955d). Selection for preweaning gain is equally effective under different nutritional regimens (Rollins and Wagnon, 1956a) even though bull calves are more adversely affected by reduced milk supply when animals are on lower feeding levels. Where conditions are desirable, bull calves gain more rapidly and reach heavier weaning weights than heifers, but under adverse pasture conditions there is little difference between bulls and heifers in weaning weights (Sawyer, et al., 1949). Good pasture conditions result in much
larger calves at weaning and a higher survival rate (Houston and Urick, 1967; Mahmud and Cobb, 1963).

Larger calves at birth gain more rapidly than smaller ones (Woodward et al., 1954a,b; Woodward and Rice, 1958); however, gains during the suckling period are not highly related to postweaning gains (Sabin et al., 1958). Two conflicting forces appear to influence the relationship between preweaning and postweaning gains. Genetic factors favoring rapid growth rate probably would give a positive relation, while compensatory gains (calves under adverse nutrition during the nursing period tend to grow more rapidly when feed conditions improve) would create a negative association of gains during the two periods (Koger and Knox, 1951; deBaca et al., 1959; Knapp and Clark, 1951; Dahmen and Bogart, 1952; Pierce et al., 1954; Willson et al., 1954; Woodward et al., 1954b; Blackwell et al., 1958; Pahnish et al., 1964).

Cobb and others (1961) found positive relationships among weights of cattle at various ages, but there was a negative association of preweaning and postweaning rates of gain. Blackwell and others (1958) found that calves from younger and older cows had lower preweaning and higher postweaning gains than calves from cows in the peak of their production. Koch and Clark (1955d) reported that selecting cows on the basis of weaning weight of their calves might increase genetic value for milking ability but would likely reduce genetic value for growth.

Heritability of postweaning rate of gain is high; consequently, selection for high postweaning gains is effective. Bulls gain more rapidly than steers and steers gain more rapidly than heifers (Bogart and Blackwell, 1950; Dahmen and Bogart, 1952), and there appears to be more variation in gain of bulls than heifers (Mason et al., 1958). Feed efficiency is closely related to rate of postweaning gains, and the factors that affect rate of gain generally affect feed efficiency (Dahmen and Bogart, 1952; Pierce et al., 1954; Woodward et al., 1954b; Lickley et al., 1960; Landers, Wheat, and Bogart, 1967). Bulls gain more rapidly and are more efficient than heifers (Nelms and Bogart, 1955; Landers, Wheat, and Bogart, 1967) even though they eat no more per unit of body weight (Ampy and Bogart, 1962; Landers, Wheat, and Bogart, 1967). Calves are more efficient in the early part of the feed test when they are small than later when they become larger. They consume more feed as they become larger but less feed per unit of body weight; consequently, relatively more feed is used for maintenance and less for growth as calves become larger (Landers, Wheat, and Bogart, 1967).

Heavier calves at birth are more efficient in converting feed into meat than lighter calves at birth. Much of the variation in feed efficiency determined on a weight-to-weight feed test can be accounted for...
Variations in birth weight, rate of gain, and weight for age at the time the test starts (Nelms and Bogart, 1955; Pierce et al., 1954). Bogart and England (1971) found that a great deal of the variation in feed conversion efficiency was accounted for by feed consumed and rate of gain.

Hohenboken and Brinks (1969) compared correcting data for environmental differences by computing from the herd data with industry correction factors. They found that the corrections from factors developed from herd data were more accurate but the differences between the two methods were small; therefore, use of the industry correction factors can be recommended because less expense is involved. Results from a study (Mangus and Brinks, 1971) in which most probable producing ability of cows was computed indicated that environmental factors reflecting high preweaning levels of nutrition had a detrimental effect upon subsequent cow productivity. There seems to be a higher relation of gain of a cow with gain of her granddaughter than gain of her daughter. Cows that gain rapidly, though reflecting desirable inheritance, will not be high milk producers because rapid gains in early life interfere with subsequent milk production. Similar results were obtained by other researchers (Kress and Burfening, 1972; Ellicott, Holland, and Neumann, 1970).

PERFORMANCE TESTING

Performance testing is an evaluation of an animal on its own performance, and progeny testing is an evaluation of an animal on the basis of performance of its offspring. Some of the early work in the United States on rate and efficiency of gains was done at the U.S. Range Livestock Station at Miles City, Montana. It was shown that rate and efficiency of gains were positively associated and under strong genetic control, and that rapid improvement could be made through selection (Quesenberry, 1950; Knapp and Clark, 1950; Woodward and Clark, 1950; Knapp et al., 1951; Haabv et al., 1952; Quesenberry, 1957).

Bogart and England (1971) showed that bulls eat no more per unit body weight than heifers but they gain more rapidly and efficiently. Lines of cattle differed markedly in daily gain, daily feed consumed, and feed efficiency. Feed consumption was found to be 0.38 heritable, which indicates that moderate to rapid changes could be made in this trait by selection. Much of the variation in feed efficiency is accounted for by variations in daily feed consumed and rate of gain. Much of the variation in daily gain is accounted for by variations in daily feed consumed and feed efficiency.

Calves have the same linear expression during different growth periods when conditions are optimum, but when fluctuations from stress
to good conditions exist, growth during one phase may be negatively related to growth of another phase (Koger and Knox, 1951; Urick et al., 1957; Kidwell, 1954). Cattle of different types have different slopes to their growth curves with the small, compact cattle gaining less rapidly than intermediate or large cattle.

Pahnish and others (1964a) reported that direct selection (selecting individuals with the best records) would be the most effective way of improving weaning weight and weaning score. Score for conformation and grade or condition could be improved by selecting for either. Roubicek (1970) also found that direct selection would be the most effective method for improving preweaning and postweaning growth. Blood studies did not indicate a need for supplemental vitamin A or phosphorus in semi-arid range areas, but control of cattle lice was found to be very important because heavy infestation with lice caused loss of red blood cells from two-year-old animals. Roubicek (1970) pointed out the advantages of putting cattle records on IBM cards for subsequent analyses.

If breeders are to improve cattle for carcass traits at a rapid rate, some methods of determining carcass merit in the live animal must be developed because progeny testing is slow and usually is done only on bulls. The use of biopsy samples for chemical composition analyses (Hawkin, Stonaker, and Cramer, 1962) or for determining muscle nuclei numbers (Herrold and Nelms, 1964) may offer promise. Nuclei numbers in muscle appear to be highly related at one time to that of another time, and nuclei numbers in early life are positively related to subsequent rate of gain.

Wagnon and Rollins (1957, 1959) estimated heritability of weight of long yearlings at 0.48 when animals were under good nutritional conditions but at -0.19 (which one assumes is zero) when feed conditions were austere. Rollins and others (1962) suggested that yearling weight of bulls was a better criterion for selection than postweaning rate of gain. Guilbert and Gregory (1952) showed that heifers reach 50 percent of mature weight at 12 months whereas bulls take 15 months to reach 50 percent of their mature weight. Kidwell and others (1952) made allometric growth studies and concluded that skeletal dimensions were more meaningful than measures of muscle and fatty development as a means of assessing growth rate.

Bailey and Almgreen (1970) compared lines selected for gains, efficiency, or conformation under high and low concentrate feeding and found that lines on high concentrate feeding gained more rapidly and produced carcasses with a higher percent of fat. It is of interest that the animals selected for conformation had larger areas of longissimus.
Jorgi muscle than the other two lines. Bailey and others (1970) selected rats for a pilot study of increased growth from 28 to 70 days under ad libitum and restricted feeding. Realized heritabilities were greater for rats selected under the higher feeding level. Also, when males from both lines were mated to control females, the young sired by males from the lines selected under high level of feeding grew more rapidly and efficiently than young sired by males from lines selected under the restricted feeding level. There were unimportant interactions of sire line x nutritional regimen, indicating little or no change in order of line response when nutritional conditions varied.

Bennett and O'Mary (1965) compared gains of calves on full feed in open lots with those housed in a barn and found that those in open lots gained more rapidly. Sellers and others (1965) found that calves born to cows on pea vine silage plus alfalfa hay were heavier at birth than calves from cows on pea vine silage alone.

Willson (1962) has pointed out that calves sired by performance-tested bulls gained more rapidly than calves sired by bulls that had no performance records and were chosen primarily on appearance. In one comparison in Montana (Thompson, 1962), steers sired by performance-tested bulls netted $16 per head more than other steers with which they were compared.

CARCASS STUDIES

Heritability estimates for slaughter grade, shrink, and certain carcass traits are presented in Table 2. Some of the estimates (Behrens et al., 1955; Lindholm and Stonaker, 1957; Harwin et al., 1961) were based on steers fed to a constant live grade. Estimates by other workers were based on steers fed for fixed periods.

The heritability estimates for most of the carcass traits are high, but direct selection for carcass traits is not possible. Progeny testing of bulls for evaluating their ability for transmitting carcass trait information and live animal measurements that are highly reflective of carcass traits can be utilized for selection purposes. The phenotypic correlations of live animal measurements and scores with carcass traits are too low to have value in selecting for carcass traits (Woodward et al., 1954a; Temple et al., 1956; Stonaker, 1958b; Brinks et al., 1962b; Hoornbeek et al., 1962). Genetic, environmental, and phenotypic correlations between production traits and carcass traits have been determined (Blackwell et al., 1962; Shelby et al., 1963; Kidwell et al., 1959a; Iwanaga and Cobb, 1963), and the relationships were generally low. In fact, Shelby and others (1963) concluded that little correlated response in carcass traits would result from selection for preslaughter traits. Kidwell
and others (1959b) concluded that flavor of muscle is associated with percent fat, average daily gain, and quality of juice as evaluated by a taste panel. Most of the research shows that rate and efficiency of gains are positively related to percent lean and negatively related to percent fat in the carcass (Stroble et al., 1951; Willson et al., 1954; Woodward, Quesenberry, and Willson, 1954a; Kidwell et al., 1959b; Woodward et al., 1959). Matthews and Bennett (1962) found that limiting the feed, which also limited rate of gain, influenced carcass quality evaluations but

<table>
<thead>
<tr>
<th>Trait</th>
<th>Heritability</th>
<th>Reference</th>
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<tr>
<td>Slaughter grade</td>
<td>.63</td>
<td>Knapp and Nordskog, 1946b</td>
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<td></td>
<td>.45</td>
<td>Knapp and Clark, 1950</td>
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<td></td>
<td>-.14</td>
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<td>.42</td>
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<td></td>
<td>.35</td>
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<tr>
<td>Shrink</td>
<td>.91</td>
<td>Knapp and Nordskog, 1946b</td>
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<td></td>
<td>.50, .53</td>
<td>Knapp and Clark, 1950</td>
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<td>Dressing percent</td>
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<td>.73</td>
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<td>.33</td>
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<td></td>
<td>-.50</td>
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<tr>
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<td>.38</td>
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<td></td>
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<td>Marbling</td>
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<td>.05</td>
<td>Harwin et al., 1961</td>
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<tr>
<td>Area of eye muscle</td>
<td>.69</td>
<td>Knapp and Nordskog, 1946b</td>
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<td></td>
<td>.68</td>
<td>Knapp and Clark, 1950</td>
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<td>.26, .46</td>
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<td>Color of eye muscle</td>
<td>-.05</td>
<td>Behrens et al., 1955</td>
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<td>.49</td>
<td>Shelby et al., 1963</td>
</tr>
<tr>
<td>Length of leg</td>
<td>.76</td>
<td>Shelby et al., 1963</td>
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<tr>
<td>Length of body</td>
<td>.46</td>
<td>Shelby et al., 1963</td>
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Differences in cutting yields and other measures of carcass value between breeds or sire groups are generally low even when dairy and beef breeds are compared (McCormick and Kidwell, 1953), but there are some breed and sire differences in amount of fat deposited when animals are slaughtered at the same weights (Ittner et al., 1952); however, animals of the same finish that are longer bodied generally produce carcasses having a higher percentage of valuable cuts (Stonaker, 1958b). Generally, differences in percent of wholesale cuts are small (Kidwell and McCormick, 1956; Stonaker, 1958b). Selection for improvement in production traits will not decrease lean meat quality, but it may be possible to develop animals which grow rapidly and deposit little fat. This would mean that beef animals slaughtered at a weight of 1,000 pounds would have carcasses of a lower grade and would need to be slaughtered at heavier weights if a higher carcass grade were deemed essential.

Urick and others (1971, 1974) found small differences in sire effects on tenderness, but there appeared to be little heterotic effects on palatability. Beef x dairy lean had less desirable flavor and tenderness than beef x beef lean. The estimated percent lean cutability was negatively associated with desirability of lean flavor, tenderness, and juice quantity and quality.

Field and Schoonover (1967) have developed a regression method for adjusting the l. dorsi muscle area of young bulls based on the linear relationship between l. dorsi area and live weight, which is \( y_i = \bar{y} - b (x_i - \bar{x}) \). The resulting equation is: l. dorsi area in square centimeters = 63.92 - 0.1307 (x_i - 348 kg live weight). From this regression equation one can compute a table of average l. dorsi areas for given live weights. This information could be important where the l. dorsi area is measured by somoscope for adjusting for size of bulls. Riley, Field, and Nelms (1966) compared tracings on acetate sheets with grid readings taken from the l. dorsi (Schoonover and Stratton, 1957) and found there was good agreement between the two methods and among persons using the two methods.

Trimmed retail cuts and their values are assumed to be a good measure of the value of a carcass. Some of the factors that influence trimmed retail cutout yield are carcass weight, weight of kidney fat, and

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1 The bar above x or y as \( \bar{x} \) or \( \bar{y} \) means the average. Without the bar above, the letter stands for an individual measurement.

2 The somoscope is a device for measuring depth of muscle by sound waves.
fat thickness over the rib eye (Cobb and Ovejera, 1964). Specific gravity of the carcass was closely related to trimmed retail cuts since specific gravity is one way to measure carcass leaness (Iwanga and Cobb, 1963). Equations were developed for predicting cutability of large and small bull carcasses so that the laborious task of cutting the carcass into retail cuts would not be necessary (Nimmo et al., 1969). The equation for larger bulls was: retail yield in kg = 12.33 + 0.73 (carcass wt. in kg) - 2.00 (fat depth in mm), and the equation for smaller bulls was: retail yield in kg = 11.79 + 0.44 (carcass wt. in kg) + 1.34 (depth of round in cm) + 0.298 (area of l. dorsi in sq. cm) - 0.85 (fat depth in mm) - 0.60 (kidney and pelvic fat in kg). These authors pointed out that no combination of factors measured gave the desired accuracy in predicting cutability. Richardson, Brinks, and Cramer (1968) pointed out that if retail values of the cuts are included, cutout value is important in developing cutability prediction equations that will truly reflect the value of the carcass.

Nolan and others (1965) found that simple linear regressions of fat, nitrogen, or moisture percentage of the standard cut 9-10-11 rib predicted total carcass composition as accurately as multiple regression equations with additional variables of depth of fat over the rib eye, rib eye area, and carcass weight included.

Carcasses from bulls and steers have been compared (Bailey et al., 1964, 1966a,b), and more lean and less fat is present in bull carcasses from animals of the same age or the same weight. There was no significant difference in shear value, but a flavor panel rated the steer carcasses over the bull carcasses in tenderness and flavors. Field, Schoonover, and Nelms (1964a, 1965) obtained consumer preferences for retail cuts from bulls and steers. They found that 89 percent of those eating meat from bulls and 91 percent of those eating meat from steers indicated they would buy the same quality of meat again. These authors also found no differences among carcasses from steers, heifers, and bulls 300 to 399 days of age, but bulls 500 to 699 days old produced carcasses that were less tender than carcasses from steers and heifers of comparable ages. Carcasses from bulls had larger loin eye areas per unit of carcass weight, less kidney and pelvic fat, a higher percentage of forequarter, and a higher percentage of the more valuable retail cuts than carcasses from steers.

For each increase in one percent of inbreeding there is a decrease of 0.19 sq. cm in l. dorsi area and 0.06 cm in depth of round (Field et al., 1966a). At the Oregon Station inbred bulls at 1,000 pounds live weight produced carcasses with more fat and less lean than linecross bulls of a comparable weight.
Garrett and others (1971) did not find a breed difference in carcass chemical composition, but there were small but significant differences in chemical composition of steers and heifers.

Carcass weight is a good indicator of muscle bone and fat in bull carcases but more accurate predictions can be made by including percent kidney fat, depth of fat over the loin, and area of *l. dorsi* in equations (Field, Schoonover, and Nelms, 1966a).

Field and others (1963) found that depth of round in the carcass was highly correlated with carcass weight, area of loin eye at the twelfth rib, length of body, and weights of *longissimus dorsi*, *semitendinous*, *superspinatus*, *infraspinatus*, and forearm muscles. Circumference of round had much lower correlations with these variables.

Cow carcases from groups under 30 months, 36 to 60 months, and over 60 months of age showed no significant difference in mean values for tenderness, juiciness, flavor, overall acceptability, shear values, and marbling score. There also were no differences between linecross and inbred cows in carcass palatability traits (Kyomo et. al., 1966).

Fat percent in muscle core samples was found to be related to fat content of the carcass, but location of sample sites is extremely important. Fat content of liver biopsy samples showed no relationship to carcass fat content.

Brinks, Clark, and Kieffer (1962b) found that ultrasonic measures of fatness are more promising as predictors of carcass traits than rib eye area. The use of photogrammetry along with live weight for predicting wholesale cuts of beef (Brinks et al., 1964a) has shown a high degree of accuracy in predicting weights of wholesale cuts but less accuracy in predicting percentages of wholesale and retail cuts.

**FERTILITY AND REPRODUCTION**

Davenport and others (1965) found that percent calf crop increased with age of cow up to 10 years. Inbreeding of 10 percent or more markedly reduced calving percentage, particularly in the younger cows. Heritability of reproductive performance was low (14 to 15 percent) for inbreds and linecrosses. Also, repeatability of reproductive ability was low. It appears that selection for reproductive performance will not be very effective.

Fagerlin, Brinks, and Stonaker (1968) studied environmental factors affecting calving interval in a Hereford herd. Highly fertile cows that calved each year had the shortest calving interval. Season of birth of calf and method of breeding (pasture, hand, and A.I.) influenced calving interval. Cows calving in spring and fall were more efficient breeders than those calving in winter or summer. Reproductive efficiency was greatest with pasture breeding and lowest with hand mating. Reimer
and Cobb (1971a) found greater mortality at birth in male than in female calves.

Breed of dam did not affect calf mortality when Hereford, Angus, and crossbred dams of these breeds were used. When Angus, Hereford, and Charolais breeds and all possible crosses among them were compared, Angus bulls sired fewer calves dead at birth than Hereford or Charolais bulls. This was presumably the result of smaller calves sired by Angus bulls. Young cows had a much greater loss of calves at birth than mature cows. Larger calves at birth were more prone to be lost at calving than smaller calves. The most productive cows in this study, as far as live calves born, were the Angus x Herefords.

Body size and pelvic area were studied in relation to calving difficulties (Bellows et al., 1971a,b, 1965b). Body weight was the most important factor associated with pelvic area but rump length and hip width also were important. Size of calf at birth contributed greatly to calving difficulties; consequently, delivery of bull calves was difficult because they were larger than heifers. Pelvic area was one of the most important factors affecting calving difficulties; the heifers with larger pelvic areas had less calving problems. Calves with longer gestation were larger and caused more delivery problems.

Warnick (1955) found the interval from calving to first estrus to be 59 days in Angus and 63 days in Hereford cattle, and age of cow had little effect on interval. Interval from calving to first estrus had little effect on fertility. It has been shown that vitamin A deficiency does not affect interval but it does delay ovulation (Christian et al., 1956). The level of feeding has a marked effect on percentage calf crop (Hubbert and Sawyer, 1951). Feeding only a limited amount of meadow hay compared with more liberal feeding reduced calf crop significantly.

Bellows and others (1968) compared feeding grain to range cows prior to, during, and prior to and during the breeding season with feeding no grain to determine the effects on reproductive performance. They found no advantage to grain feeding as long as range forage was adequate but pointed out that problems could arise with a shortage of good forage because cows draw material from their bodies for milk production.

Ray and Roubicek (1971) tried flushing heifers grazing on desert range for 97 days, starting 30 days before the beginning of the breeding season. The heifers on range without concentrate supplement had a slightly higher calving percentage than those that received supplement. The calves from the supplemented heifers did not gain more rapidly during the nursing period, which indicates that supplementation at breeding time did not increase milk production. Heifers on supplement grazed less because they depended on limited supplementation; consequently
their energy intake was not increased. These results agree with studies by Bellows and others (1965a), who gave supplemental grain for 137 days to see if this would stimulate puberty in beef heifers. The supplement-fed heifers gained more, but did not have larger pelvic openings or reproductive tracts. They did show puberty 16 days earlier than non-supplemented heifers. Bellows and others (1970) superovulated heifers by use of hormones following synchronization of estrus. Five of thirty-four treated heifers produced twins. Gestation length and calf size were greater for singles than for twins. Calves from the treated cows were weaned early and artificially reared. The interval from calving to first estrus was 16 to 23.8 days when calves were weaned at 3 days, 19 days when calves were weaned at 10 days, and 43 days when calves were allowed to nurse.

Losses of calves at or shortly following birth were reported (Anderson, 1968; Bellows, 1965) at about 5 percent in a straightbred Hereford herd. More bull calves than heifers were lost at calving and losses were greater in younger than in mature cows. Since about 80 percent of the calves lost at birth were anatomically normal, the greatest cause of calf loss was injury at birth. About 70 percent of the calves lost at birth had not breathed.

From 11,527 calvings, 51.4 percent were males and 48.6 percent were females (Clark et al., 1963). Mortality at birth was higher (59.5%) in males than in females (40.5%), but mortality following birth was slightly higher in females than in males. At time of weaning, 51.3 percent of the calves were males and 48.7 percent females. There was no relationship of age of dam with sex ratios of calves.

Certain specific sex-limited autosomal genes cause sterility in cows (Gregory et al., 1951b; Kidwell et al., 1954); in addition, prolonged gestation (Gregory et al., 1951a) and double cervix (Sittman et al., 1961) are inherited as simple recessives. Length of gestation is affected by additive genes of both the calf and the dam, the two traits being about equally heritable at 30 percent (Rollins et al., 1956). Calving interval has essentially zero heritability and repeatability (Brown et al., 1954), which means that selection for this trait would be ineffective. Christian (1957) found that beef heifers reach puberty at about 12 months of age but show follicular development and may ovulate prior to first estrus.

Brinks and others (1964c) found that phenotypic, genetic, and environmental correlations of weights and gains from birth through maturity with most probable producing ability (MPPA) were all small. The best single predictor of producing ability was weight at 18 months of age.

\[ MPPA \] is a calculated producing ability that one would most probably expect from a cow.
It appears that fertility of some yearling bulls is not adversely affected by high levels of feeding (Bennett, Ehlers, and O'Mary, 1965). The fact that yearling bulls are growing probably prevents excessive feeding from harming reproduction because the young bulls grow more but fatten less than more mature bulls when heavily fed.

McNitt, Stonaker, and Carroll (1966) found sperm concentration to be 0.37 heritable while the heritability of sperm vigor, percent alive, and morphology was essentially zero. Defects of the reproductive tract were not specific for lines except that testicular hypoplasia occurred in only 3 of more than 12 lines. Semen quality was lower for inbred than for linecross, crossbred, and outbred bulls, and the lower quality of semen was more pronounced as inbreeding increased.

Fagerlin, Carroll, and Brinks (1971) studied growth of young bulls in relation to scrotal circumference (Figure 1) and semen quality.

Figure 1. Method of measuring scrotal circumference in young bulls. (Courtesy J. S. Brinks, Colorado State University.)

Scrotal circumference was highly related to body size in the early phases but this relationship became less as bulls approached the end of the feed test. Scrotal circumference taken at the end of the first month of the feed test was more highly correlated with subsequent semen data than scrotal circumference taken earlier or later. Scrotal circumference showed a higher linear regression on weight than on age of young bulls.
Crossbred bulls showed sperm in the ejaculate earlier (228 vs 243 days), motile sperm earlier (248 vs 285 days), earlier age at first ejaculation (288 vs 313 days), and earlier age at fertile sperm production (355 vs 397 days) than straightbred bulls (Bellows et al., 1964). In addition, libido or sex drive was greater for crossbred bulls. Angus-sired calves reached sexual activity earlier than Hereford and Charolais-sired bulls. Breeding ability was reached at the oldest age for Charolais-sired bulls.

Semen collected by artificial vagina has higher sperm concentration and contains more fructose and citric acid than semen collected by electro-ejaculator, but there are no other differences in semen collected by these methods (Cupps et al., 1957). It has been thought that if semen could be collected from young bulls and frozen, the bulls could then be slaughtered and their carcasses evaluated before the semen was used. Unfortunately, after freezing, semen from young bulls gave only a 25 percent conception rate (Salisbury et al., 1960), which makes this procedure unworkable.

RELATIONSHIPS AMONG TRAITS

Scores for type and conformation and body measurements show little or no relationships with preweaning or postweaning rates of gain (Knox and Koger, 1946; Knapp and Clark, 1951; Knox et al., 1951; Durham and Knox, 1953; Woodward et al., 1954a,b; Bogart et al., 1955, 1956; Koch and Clark, 1955b; MacDonald and Bogart, 1955; Knox, 1957). In fact, negative phenotypic associations (Hoornbeek et al., 1962) and negative genetic associations (Romo and Blackwell, 1954) were found between grades or scores at weaning and subsequent gains.

Scores for type and conformation at weaning do not serve as predictors of subsequent production performance and scores at slaughter do not accurately predict carcass desirability (Kidwell et al., 1959a,b; Knapp and Clark, 1951; MacDonald and Bogart, 1955; Koch and Clark, 1955b; Durham and Knox, 1953; Romo and Blackwell, 1954; Bogart et al., 1956; Bogart and Frischknecht, 1967). There is evidence that type and conformation can be altered through selection (Pahnish et al., 1961a; Ternan et al., 1959; Shelby et al., 1955; Kidwell et al., 1959b; Rollins and Wagnon, 1956b).

Bogart and others (1956) found that calves on a weight-constant basis that are smaller in heart girth and longer in body grow more rapidly and efficiently, but Kidwell and others (1959a) pointed out that many of the correlations involving body measurements are often the result of differences in size of the animal where a weight-constant basis is not used. It appears that selecting longer bodied animals would be desirable.
Bailey and others (1971) studied cattle selected for gain, for efficiency, and for conformation. Part of the cattle were kept under irrigated pasture conditions, while part were under desert range conditions (Figure 2). The genetic correlations observed in this study indicate that selection for rate of gain or for rate of feed efficiency should result in improvement of the other.

A great amount of concern was given to type studies. Some of the differences in results obtained when cattle were compared were due to differences in methods of comparison. When composted and conventional cattle were fed to a constant condition of low choice grade there was little difference between the two types in feed conversion efficiency and carcass composition (Stonaker et al., 1952), but when they were fed to the same slaughter weights, larger type cattle grew more rapidly and economically and produced carcasses with more lean and less fat than compost cattle (Kidwell and McCormick, 1956; Knox and Koger, 1946). Knox (1954, 1957) showed that lifetime production and production per 1,000 pounds of cow were greater for larger type cows. He further pointed out that many of the costs of production are on a per-head basis which favors larger type cows. Stonaker and others (1952) showed that winter feed consumption was related to body weight and favored the smaller type cattle. Washburn and others (1948) found that food capacity was related to size and that there was no difference in digestibility of compact and conventional cattle. The conventional cattle tended to grow more while the compact cattle tended to fatten.

Larger cows tend to produce calves that grow more rapidly during the preweaning and postweaning periods (Sawyer et al., 1963; Brinks et al., 1962a), and there is an indication that cows gaining more during the winter and losing more during the suckling period produce heavier calves at weaning. Brinks and others (1962a) found that selecting for gains during one period would not materially reduce progress from selection for gains in the other periods.

Heifers that grow during the nursing period tend to have lower productivity as cows than heifers growing less rapidly. This gives a negative relation between suckling gains of dams and offspring. It appears that there is a negative or antagonistic relationship between additive direct and additive maternal effects on growth (Hohenboken and Brinks, 1971a,b; Mangus and Brinks, 1971), but this relationship is not so large as to prevent progress from selection for growth. It does result in a cyclic phenomenon in which high weaning weights of calves is more closely associated with high weaning weights of granddams and with lower weaning weights of the dams. Inbreeding tends to reduce the most probable producing ability of cows.
Figure 2. Cattle under range conditions at Knoll Creek, Nevada (top). Cows under irrigated pasture conditions at Reno, Nevada (bottom). (Courtesy C. M. Bailey, University of Nevada.)
Hoornbeek and Bogart (1966) studied changes in performance traits in three one-sire Hereford lines and one two-sire Angus line. In the small one-sire lines, rate and efficiency of gains and scores for conformation initially improved from selection, followed by a plateau and a decline. Preweaning gains declined with no indication of selection preventing the depressing effect of inbreeding. There was selection against inbreeding even though there was no conscious effort to keep or cull more highly inbred animals. Selection differentials were much higher in bulls than in heifers. The Angus line showed that inbreeding depression could be prevented in all traits by selection in a larger population in which inbreeding is less intense.

Nelms and Stratton (1967) evaluated the effect of selection for yearling weight. They had a selection intensity of 0.19 standard deviation or 24.1 kg per generation. Their results show clearly that yearling weight can be improved by selection.

Brinks, Clark, and Kieffer (1965) studied changes in a herd from 1934 to 1959. Inbreeding increased to about 22 percent, with an average inbreeding of 19 percent over the entire period. Inbreeding depressed production traits of the calf and inbreeding of the dams caused lower weaning weights of their calves, presumably due to reduced milk production. In general, selection was toward lower inbreeding of both the calf and the cow but the breeding system employed brought about an increase in inbreeding in spite of selection for lower inbreeding. Selection differentials were high for sires for all production traits and positive but not high for most of the traits in the females. Calculated values for genetic change derived from estimated heritabilities, genetic correlations, and relative weights showed that all traits should improve. Phenotypic changes calculated as regressions of annual mean values of the traits on years showed strong positive changes except for gain from weaning to 12 months in heifers, which showed no change. Environmental changes showed some decline over the period of the study. There was substantial genetic improvement of 9.7 pounds in birth weight, 21 pounds in gain from birth to weaning, 30 pounds in weaning weight, and 6.5 percent in weaning score. There was more actual improvement made than expected, especially between 1943 and 1959.

Flower and others (1964) analyzed data on selection intensities and time trends in inbred lines of Herefords. Selection was intense on the sire side for weaning weight, postweaning rate of gain, and final weight at end of test. Direct selection for combining ability in the recurrent selection was low. Phenotypic time trends showed a negative response in heifers and in environmental trends. When genetic progress was measured...
by removing the negative time trend for environment, positive progress was somewhat greater than expected. Where selection was most intense, progress was greatest. Armstrong and others (1965) studied selection intensity and genetic progress from time trends and found that environmental trends increased whereas genetic trends decreased for all traits except feed efficiency. The lines of cattle in this study were small and perhaps inbreeding depression was greater than selection could overcome. With a somewhat similar line, Nelms and Stratton (1964) obtained modest improvement of all production traits through selection.

Gregory, Shelby, and Clark (1963) studied weights of cow progeny selected or rejected for breeding. They obtained a ratio of 2 selected: 1 rejected early in life: 1 rejected later in life.

Bogart and others (1963a) determined heritability of yearling weight of cattle under restricted and improved postweaning feeding levels by regression of offspring performance on dam performance. The regressions were much higher when animals were under better feed conditions, indicating that one might make more improvement by testing under a good environment representative of normal producer conditions.

Genetic parameters indicate that modest to marked improvement could be expected from intense selection for production traits. There are also some genetic correlations among growth factors and feed efficiency which should lead to some correlated response from selection (Blackwell et al., 1962; Pahnish et al., 1963; Brinks et al., 1964c; Shelby et al., 1963; Roberson et al., 1963). The correlation of most probable producing ability with preweaning growth is negative (Ellicott, Holland, and Neumann, 1970), indicating that cows out of young and old dams have below average preweaning performance but produce calves that are above average in preweaning performance.

INBREEDING

Several closed breeding populations, varying greatly in size, have been established (Urick et al., 1966) and selection for production traits has been practiced in all lines; consequently, it has not been possible in most studies to clearly separate the inbreeding and selection effects. Most of the studies show that inbreeding of the calf results in a depression in preweaning and postweaning rates of gains (McCleery and Blackwell, 1954; Burgess et al., 1954; Blackwell et al., 1957). In general, inbreeding depression is more marked for the lowly heritable traits (suckling rate of gain) than for the highly heritable traits (postweaning rate of gain, scores, and feed efficiency), which indicates that selection may prevent the depressing effect for highly heritable but not for lowly heritable traits (Alexander and Bogart, 1959, 1961; Moore et al., 1958).
Inbreeding also reduces fertility (Harris et al., 1960) in young bulls, partly because of a delay in sexual maturity. There is a much higher percentage of stillbirths and deaths in early life among inbred than among outbred or linecross calves (Woodward and Clark, 1959; Theurer, Stonaker, and Riddle, 1966; Humes, 1968).

There is some evidence that inbreeding of the calf has a more depressing effect on growth in females (Figure 3), while inbreeding of dam has a greater effect on males. It is presumed that inbreeding of the dam causes her to produce less milk and that the reduced milk supply affects male calves more than female calves (Brinks, Clark, and Kieffer, 1963).

Inbreeding does not appear to reduce mature body size in the herds in which inbreeding exceeds 30 percent in only a few animals. Stonaker (1951) described a herd that had been closed for a sufficient time to increase the inter se relationship among animals in the herd to a level that was greater than that between full sibs. There was some evidence of reduction of mature body size in this herd.

Stonaker (1962) pointed out that lethals and abnormalities have not appeared at a high frequency in inbred lines even when inbreeding has exceeded 30 percent, but there is a marked reduction in calf crop from inbred cows. Calves in closed lines are smaller at birth and lines differ...
greatly in all performance traits. He indicated from his economic analysis that weaning weight is more important than postweaning rate and efficiency of gain. In evaluating performance, there have been marked differences between years in all performance traits. Daily gains of bulls on test are more affected by initial weight than by age, inbreeding, or age of dam. He suggests that cattlemen should select replacement heifers and bulls from better producing cows.

**HETEROSIS AND COMBINING ABILITY**

Heterosis has been evaluated where inbred bulls have been top-crossed onto unrelated outbred cows, in crosses between inbred lines, and in the crossing of different breeds. Hoornbeek and others (1962) tested performance-tested sires from four closed lines of Herefords on commercial cows. Calves from the four lines of sires differed in performance traits but no single line excelled in all traits. There was general agreement between relative performance of the lines and relative performance of the calves sired by bulls from the various lines. Bulls that excelled in a particular trait sired calves in the commercial herd that excelled in that trait. Sires from one line produced calves with the most rapid rate of gain, sires from two other lines produced calves with the highest USDA grade, while sires from the fourth line produced calves that were generally inferior (Bogart, McArthur, and Hoornbeek, 1967).

The Arizona Station conducted topcross tests comparing the progeny of sires from several Montana-developed inbred lines with the progeny of sires from private herds (Pahnish et al., 1962). The progeny by sires from one Montana line showed an advantage of 2.5 percent in weaning weight over the average of the calves by the non-inbred sires. Yearling weight advantages of 5.5 percent and 4.0 percent (bull and heifer progeny, respectively) in favor of stock sired by inbred bulls of one line were reported. The bull and heifer calves making the greatest postweaning gains were by one of the inbred sires. While this progeny group weighed only about 5.4 percent more than the herd average at weaning time, gains from weaning to fall yearling age were 15.8 percent and 6.0 percent above the herd average for bull and heifer progeny, respectively. There was little practical difference in the grades and condition scores of progenies sired by the inbred and non-inbred bulls.

A comparison was made of calves sired by bulls from a closed herd selected for performance with those sired by bulls from an outbred herd in which sires were selected visually. The calves from the bulls in the line that was performance tested were superior in performance to those sired by bulls from the other population (Willson et al., 1963). Ray and
others (1968, 1970) also compared performance of progeny from three
topcross sire and dam lines and an industry herd. The line of dam exerted
a greater influence on preweaning performance than line of sire, while
line of sire had a greater influence on postweaning performance. There
was a negative relation between preweaning and postweaning growth.
There was also a negative relationship between maternal ability and
growth potential among the topcrosses.

A study on maternal heterosis in postweaning traits (Brinks et al.,
1971) showed a strong heterotic effect from use of linecrosses over inbred
dams for calf production. Three-way crosses where the dams were line-
crosses were superior to three-way crosses where dams were inbreds. The
heterotic advantages varied from 2 to 12 percent for the various traits
among the different combinations. The greatest heterosis was expressed
when linecross dams were mated to an inbred bull of a different line for
weaning weight of all calves (12%) and 12-month weight of heifers (11%).

Cows sired by bulls from four different inbred lines were compared
for their calf-producing abilities (McArthur, Bogart, and Humes, 1967).
One line sired heifers that grew slowly and were small for breeding to
calve as two-year-old cows. The result was low conception and low
weaning weights of the calves; consequently, calf production from cows
sired by this line was markedly inferior to production from cows sired
by bulls of the other three lines.

Flower and others (1963) compared three inbred lines of Herefords
and their crosses with a common inbred tester line. Growth rates of inbred
lines were highly predictive of growth rates of their linecross progeny.
Hybrid advantage varied by trait from 0 to 5%, with final weight showing
the greatest hybrid advantage. Heterosis for postweaning growth result-
ing from crossing five inbred lines of Hereford cattle (Urick et al., 1968)
varied in body weight from one period to another (4.5 to 7.3%) and in
gains made during a period (2.2 to 13%).

Humes and others (1973) and Humes, Bogart, and Schilling (1969)
studied preweaning performance from a diallel mating of three inbred
lines of Herefords. They observed no line of sire x line of dam interaction,
which suggests no specific combining ability effects for preweaning and
weaning traits. One line showed superiority when either sires or dams
were crossed with the other two lines, indicating some general combining
ability.

Brinks and others (1967) found that there were more heterotic effects
for preweaning daily gains and weaning weights than for birth weights
and weaning scores when crosses among five inbred lines of Herefords
were studied. Heifers showed more heterosis than bull calves for pre-
weaning rate of gain and weaning weights. Heterotic effects varied fro
2.5 to 5.6 percent in bulls and from 2.7 to 10.6 percent in heifers for the four traits considered.

Stonaker (1962, 1963) reported that heterosis is much higher in female cattle and in male chickens than in the opposite sexes, which suggests that much of the heterosis is associated with the genes located in the x-chromosome. He proposed the idea of homogametic heterosis or hybrid vigor in the xx sex due to heterozygosity in the homogametic sex which could not exist in the heterogametic sex. Theurer, Stonaker, and Riddle (1966) reported that inbreeding causes greater mortality in female calves than in males and that homogametic heterosis for survival was evident because greater survival was shown in linecross females than in linecross males. They found that the calf having the greatest chance for survival until weaning is a linecross male out of a mature dam and born during the middle of the calving season. Calves with the least chance of survival are inbred females (born early in the calving season) out of two-year-old dams.

Brinks (1965) pointed out that the greatest economic advantage of crossbreeding is the number of calves weaned per 100 cows bred because crossbreeding results in greater conception and in greater survival of calves born. Hybrid vigor is greater in preweaning growth (3-6%), but it is also evident in postweaning growth. Feed conversion efficiency (Figure 4) shows little effects of hybrid vigor, but overall efficiency would be greater for crossbreeds if all animals were marketed at the same weight since less time would be required for getting them to market weight. Most carcass traits that are not associated with differences in rate of gain show no hybrid vigor when breeds are crossed. Management and selection programs may have to be modified to utilize fully a planned and systematic crossbreeding program.

Bogart (1966) pointed out that more hybrid vigor could be expected from crossing breeds than from crossing lines within a breed. There is also a possibility of capitalizing on the strong points of two breeds when they are used for terminal matings in which all offspring are marketed. Here one would want cows of a breed that is high in fertility and milking ability bred to bulls with high rate and efficiency of gains and desirable carcass characteristics. The rotational crossbreeding program in which three breeds are used offers promise because it takes advantage of heterosis in the production of calves for market.

Rollins and others (1969) compared crosses among Hereford, Angus, and Shorthorn breeds and found that hybrid vigor for weaning weights and percent calves weaned was: Hereford x Angus, 7.0 kg and 15 percent; Hereford x Shorthorn, 10.2 kg and -8 percent; and Angus x Shorthorn, 5 kg and 14 percent. Later, Rollins and others (1970) compared calves
Figure 4. Feed conversion efficiency requires individual feeding. Individual pens may be used (top) or animals may be tied or stanchioned at time of feeding (bottom). (Courtesy C. M. Bailey, University of Nevada, and J. S. Brinks, Colorado State University.)
where crisscross matings were involved using Herefords and Angus and
found the reciprocal backcrosses 8.1 percent higher for percent calves
weaned and 9.7 percent higher for weaning weight than for averages
of the straightbreds.

Reimer and Cobb (1971a,b) studied preweaning records of straight-
bred and crossbred calves sired by Angus, Hereford, and Charolais bulls
and produced by Angus and Hereford cows (Figure 5). Calves sired
by Charolais were consistently heavier at birth and weaning than

Figure 5. Angus cow herd (top) and Hereford cow herd (bottom) at the Mealani
Experiment Station, Kamuela, Hawaii. (Courtesy D. Reimer, University of Hawaii.)
the other calves. Hereford cows had heavier calves than Angus at birth, but gains during the nursing period were greater for calves from Angus cows. The ranking for weaning weights and suckling gains were: Charolais x Angus, Charolais x Hereford, Hereford x Angus, Angus x Hereford, Angus x Angus, and Hereford x Hereford. The Charolais-sired calves showed superiority over straightbred calves for suckling gains (16%) and weaning weights (18%).

Calf performance to weaning of beef x beef and beef x dairy breeds (Pahnish et al., 1969a) gave heaviest weaning weights and the greatest suckling gains when Brown Swiss cows were bred to Hereford, Angus, or Charolais bulls. The average advantage in weaning weights of calves from Brown Swiss dams over dams of the three beef breeds was 33.6 kg for bull calves and 32.5 kg for heifer calves. Steer calves exhibited greater heterosis than heifer calves for each of the traits considered.

Kieffer and others (1962) compared straightbred and crossbred steers and found that Charolais x Hereford steers were superior to their straightbred contemporaries for both preweaning and postweaning performance traits. Hereford steers graded higher in the carcass and were more tender than Hereford x Charolais steers. Charolais steers yielded the highest percent of lean and the lowest percent of fat, while the Hereford steers had the highest percent fat and the lowest percent lean in the carcass. Brown Swiss steers grew most rapidly during the preweaning period but not as rapidly as the Hereford x Brown Swiss steers during postweaning.

Several studies have been made in which breeds have been crossed. In many of these studies, Brahman breeding has been employed in the crosses. Hubbert and others (1955) compared Herefords with Hereford x Brahman crossbreds in eastern Oregon and found that the Herefords made more rapid gains in the feedlot but did not equal the crossbred in rate of gain on the summer range. Final weights were slightly in favor of the crossbreds. Rollins and Ittner (1956) compared Herefords with Brahford (% Hereford and % Brahman) and found that the crossbreds gained more rapidly during the summer when temperatures were high and reached greater final weights. Efficiency was in favor of the Herefords. Differences between the groups were not large. Carroll and others (1955) compared Herefords with Brahman x Hereford crossbreds and found that Herefords gained more in the feedlot (2.16 lbs. per day compared with 1.90) and required less feed per 100 pounds of gain (843 lbs. compared with 929 lbs.) even though initial weights of the two groups were practically identical.

The California researchers compared Herefords with % Brahman-% Hereford (Carroll et al., 1964) and found that crossbred steers pro-
duced carcasses that had a higher dressing percent, produced darker meat that was less tender, and showed some indication (barely significant) of less juiciness than carcasses produced by Hereford steers. The crossbred steers outgained the Hereford steers during the summer, but the Herefords outgained the crossbred steers during the fall and winter when there was no heat stress. Body temperatures were higher for the Herefords than for the crossbreds during the summer (Rollins, Carroll, and Ittner, 1964). Also, Hereford x Charbray and Hereford x Charolais calves were compared with purebred Herefords and Charbrays (Carroll and Rollins, 1965). There was more drip loss in cooking meat from the purebreds and greater shear values (indicating less tenderness) in meat from the crossbreds, but a taste panel found no differences in tenderness, flavor, or juiciness.

Knapp and others (1949) and Quesenberry (1950, 1957) compared Herefords with first-generation crossbreds (Shorthorn bull x Hereford cows), second-generation crossbreds (Angus bull x first-generation crossbred cows), and third-generation crossbreds (Hereford bull x second-generation crossbred cows). All crossbred steers gained more rapidly than the Herefords during both suckling and feedlot periods, but feed efficiency was not markedly different for the different breeding groups. Growth rate of the females was greatest for the second-generation females up to 18 months of age, but first-generation females reached the largest mature size. Growth up to weaning increased with increases in crossbreeding generations. This may reflect heterotic effects on milking ability of crossbred dams rather than growth potential of the calves. The fact that first-cross heifers were the largest at maturity but not at 18 months of age would indicate that they had great growth potential but did not enjoy a maternal environment which would permit full expression of their growth potential up to weaning.

Pahnish and others (1969b) studied postweaning performance of progeny from straightbreds Hereford, Angus, and Charolais; the six reciprocal crosses; and beef bulls x Brown Swiss cows. The greatest heterotic effect was in average daily gains from weaning to yearling ages. The heterotic effects were small for most of the traits considered. The beef x Brown Swiss had outstanding gains particularly during the nursing period but they graded lower than beef x beef crossbreds. In another study in which Hereford, Angus, and Charolais steers were compared with the crossbreds among these three breeds, the crossbreds had higher initial weights, daily gains, and heavier weights after feeding for 112 days than straightbreds but feed efficiency was the same for the two groups. For the entire feeding period, the heterotic advantages of the crossbreds were 3.7 percent for daily gain, 3.3 percent for feed efficiency, and 1.1 per-
cent for carcass grade. It required 11 days less feeding time to finish crossbred than straightbred steers (Pahnish et al., 1970).

Kearl (1971) made an economic study of crossbreeding and the methods of moving into a crossbreeding program. His studies show substantial advantages—16 to 20 percent increases in net income after taxes—are likely to accrue from use of crossbreeding. Possible increases in calf crop of 5 percent in the first cross and 6 percent in the second cross are conservative estimates, based on a calf crop of around 83 percent.

The calf crop increase attainable on ranches with average or below average performance might actually be considerably better than 5 or 6 percent. This is particularly true if crossbreeding effected much more widespread and successful calving of two-year-old heifers with a considerably higher percentage calf crop from those animals. The result is likely due to the greater growth rate in young crossbred animals and to earlier sexual maturity.

Projected increase in average weights of 5 percent at the first cross and 10 percent at the second cross of yearlings is reasonable. This is consistent with much of the experimental evidence previously shown. Weights of 640, 672, and 704 pounds for yearling heifers and 705, 740, and 775 pounds for yearling steers were used for straightbred, first-cross, and second-cross animals.

Some of the work of the Montana Station is summarized in Table 3, showing small but important heterotic effects, particularly for weaning weight, preweaning gains, and yearling weight. In general, their figures show that preweaning and postweaning gains are increased 3 to 7 percent by systematic crossbreeding.

<table>
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<th>Trait</th>
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<tr>
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</tr>
<tr>
<td>Postweaning ADG (heifers)</td>
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<td>Yearling weight (heifers)</td>
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<tr>
<td>Birth weight</td>
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<td>Burfening and Kress, 1973</td>
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<td>180-day weight</td>
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<td>Postweaning ADG</td>
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<td>Yearling weight</td>
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<td>MPPA for birth weight</td>
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<td>Birth weight</td>
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<td>Anderson et al., 1973</td>
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<tr>
<td>180-day weight</td>
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<td>Yearling weight</td>
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INTERRELATIONSHIPS BETWEEN GENETICS, METABOLISM, AND ENDOCRINE PHYSIOLOGY

Biochemical constituents such as urea nitrogen, uric acid, amino acid nitrogen, creatine, ammonia nitrogen, and creatinine in the blood and/or urine of calves during the growing period show that urea nitrogen and amino acid levels in the blood and urea nitrogen levels in the urine increase as calves become older and larger and that heifers of comparable ages have higher levels than bulls. Also, more rapidly and economically gaining calves have lower urea and amino acid nitrogen levels than slowly gaining calves. There are line differences in blood constituents. It has been speculated from the studies by the Oregon researchers that rapidly gaining cattle have the capacity to utilize amino acids from the bloodstream for building muscle tissue while slowly gaining animals must eliminate amino acid material by deaminizing, excreting the nitrogenous material as urea and using the carbonaceous fraction as a source of energy (MacDonald et al., 1953, 1956; Krueger et al., 1956; Price et al., 1956; Ampy and Bogart, 1962; Johnston et al., 1962; and Bogart et al., 1963b).

Collection of urine from both heifers and bulls was made possible by use of an apparatus for collecting urine and feces separately from heifers, developed by Mason and others (1956c). Normal values, changes with age, and differences due to sex have been established for hemoglobin, hematocrit, red cell counts, red cell volume, and white cell counts (Price et al., 1957, 1959; Alexander et al., 1959). The amount of hemoglobin per unit volume of blood, content per red cell, and concentration in the red cells increases as calves become larger, while the number of red cells decreases with increases in body weight (Bhamasiri, Bogart, and Krueger, 1964). Rice, Nelms, and Schoonover (1967) found that injectable iron given at birth or at two months of age may increase hemoglobin levels and slightly stimulate growth of calves.

Normal values for percentages of albumen, alpha globulin, beta globulin, and gamma globulin at 500 and 800-pound body weight have been established (Price et al., 1959). These values do not vary with size or sex, but percent of gamma globulin is positively associated with rate of gain (Ampy et al., 1961).

Roubicek, Ray, and Hale (1970) studied creatinine and uric acid levels in the blood of range cattle at various ages. The heritability of these blood constituents was zero. Year and sex effects on them were significant. The relationship of levels of these constituents at four ages was low, indicating considerable fluctuations in values for these constituents. There were negative associations of creatinine concentration with weights at 340 and 600 days. Total serum protein and protein fractions (alpha,
have larger amounts of gonadotropic pituitary glands than slowly gaining animals (Burris et al., 1953a,b, 1954; Krueger et al., 1954). Beef cattle that were fed rations low in protein (potatoes and straw) had the same amount of thyrotropic hormones in their pituitary glands as those fed a standard ration (Nicholson et al., 1962). Parl et al. determined follicle-stimulating hormone (FSH) and luteinizing hormone (LH) concentrations in pituitaries from bulls and steers and found that FSH concentration was very low. In fact, the total of FSH in pituitaries of rats and bulls is about equal. LH concentrations were fairly high in bulls but much lower in pituitaries from steers. The FSH concentrations were higher in steers than in bulls. This study shows clearly that large differences among species exist.

Taylor and others (1966) found that sex and year of birth influenced serum cholesterol levels. There was little relationship between serum cholesterol level and performance traits. Heritability of cholesterol concentration varied from zero to 0.46, depending on sex and size (Taylor et al., 1963). Genetic correlations of cholesterol concentration at 235 days with 600-day weight and daily gain from birth to 600 days were 0.60 and 0.59, respectively. Plasma phosphorus levels of range calves showed marked variation from one sampling to another and apparently were influenced by forage quality (Roubicek et al., 1968). The heritability of plasma phosphorus levels was low, and there was low relationship of phosphorus levels with growth rate.

Hepatic (Figure 6) and blood concentrations of carotene and vitamin A in range cattle in the San Carlos, Arizona, area were generally higher for females than for males and there were large year effects. Heritability estimates varied between periods estimated and were generally higher when forage conditions were better. There were small and unimportant correlations of hepatic and blood concentrations of carotene and vitamin A with growth (Taylor, Pahnish, and Roubicek, 1968).

Endocrine studies have shown that more rapidly gaining animals have larger amounts of gonadotropic and thyrotropic hormones in their pituitary glands than slowly gaining animals (Burris and Bogart, 1953; Burris et al., 1953a,b, 1954; Krueger et al., 1954). Beef cattle that were fed rations low in protein (potatoes and straw) had the same amount of thyrotropic hormone in their pituitary glands as those fed a standard ration (Nicholson et al., 1962). Parlow, Bailey, and Foote (1973) determined follicle-stimulating hormone (FSH) and luteinizing hormone (LH) concentrations in pituitaries from bulls and steers and found that FSH concentration was very low. In fact, the total of FSH in pituitaries of rats and bulls is about equal. LH concentrations were fairly high in bulls but much lower in pituitaries from steers. The FSH concentrations were higher in steers than in bulls. This study shows clearly that large differences among species exist.

Lucas and others (1950) found that small-type steers had smaller endocrine weights than larger steers. They also noted that thyroid and adrenal weights were correlated with rate of gain. Carroll and other
(1951) found less thyrotropic hormone in pituitaries of dwarf calves than in pituitaries of normal ones, but Cornelius and others (1956) found that protein-bound iodine levels of dwarfs and normals were the same. This indicates that dwarf cattle are not cretins. Galgan and others (1956a,b) reported higher rate of gain associated with lower effective half-life of radioiodine, but Ham and others (1954) were unable to find a relationship of protein-bound iodine and rate or efficiency of gains.

Bulls gain more rapidly and efficiently than heifers (Bogart and Blackwell, 1950; Dahmen and Bogart, 1952); consequently, investigations on the influence of injected testosterone into heifers and steers were made. At a calculated level of normal production (1 mg/kg/week), testos-
terone increased rate of gain 0.5 pound per day in heifers and 0.1 pound per day in steers and decreased feed required per 100 pounds gain by 180 pounds for heifers and 41 pounds for steers. Testosterone injections resulted in marked masculinization, a marked increase in muscle development, and a reduction in fat deposition. The carcasses from treated and control animals were acceptable by taste panel evaluations.

Testosterone administration altered the hormone content and size of certain endocrine glands (Burris and Bogart, 1953; Burris et al., 1953a). In the pituitary gland, gonadotropic hormone content was decreased while the thyrotropic hormone content was increased by testosterone treatment. Thyroid glands from animals treated with testosterone were larger than thyroids from comparable controls.

Testosterone-treated heifers did not ovulate (Burris et al., 1954; Krueger and Bogart, 1959) as readily as controls (20% vs 100%). Heifers that had received testosterone ovulated 30 days following cessation of testosterone treatment and became pregnant. Continued testosterone treatment during pregnancy resulted in one calf, presumably a female, that had abnormal genitalia showing pronounced Freemartin characteristics (Floyd et al., 1957; Mason et al., 1957, 1958; Bogart et al., 1958). It was presumed that testosterone crossed the placenta and entered blood circulation of the calf.

When fed at various levels, methyl testosterone did not alter rate and efficiency of gains, but it did influence endocrine glands and accessory sex organs (Krueger et al., 1954).

North (1966) used ovarian fragments from frogs in a culture medium and noted the number of eggs ovulated as a means of assaying pituitary material for gonadotropin. He found pituitary material from cattle rather ineffective for causing frog ovarian tissue to release eggs, but pituitary material was more effective when it received 1,000 to 5,000 r of x-irradiation. Mason and others (1956a,b) reported that inheritance, nutrition, and endocrines are interrelated in their effects on growth and well-being.

Glutathione levels in the blood were not good indicators of subsequent rate and efficiency of gains in growing cattle (Kidwell et al., 1959a; Kidwell, 1955). Serum alkaline and acid phosphatase activities were found to be positively related to subsequent rate of gain in calves. In addition, the ratio of acid to alkaline phosphatase activity and the uniformity of levels of activity in an animal were related to growth rate and feed efficiency (Alexander et al., 1958; Johnston et al., 1961, 1962).

Anwar-Afghan (1967) studied nicotinamide adenine denucleotide coenzymes of the liver in relation to production traits. It was found that liver coenzymes concerned with fat metabolism were positively related to percent fat in the carcass and to inbreeding percentage but negatively
related to rate of gain, percent lean in the carcass, and size of the thyroid gland.

Blood group studies (Stroble et al., 1954; Mason and Stroble, 1954; Stroble and Hilston, 1955) show blood group differences between lines but no relationship of blood groups with performance traits.

One might assume that one reason for differences in rate and efficiency of gains would be differences in digestibility of feed; however, when over 60 animals were given the same feed consisting of two parts alfalfa to one part of a concentrate mixture, Nelms and others (1954, 1955) were unable to find any relationship between digestibility and rate or efficiency of gains.

Heart function has been studied from electrocardiograms taken on normal animals at various ages, those suffering from white muscle disease, those with heart anomalies, and on those of the various dwarf complex (Krueger and VanArsdel, 1959; VanArsdel et al., 1960a,b; VanArsdel, Krueger, and Bogart, 1963; Krueger, VanArsdel, and Bogart, 1960). Heart sounds have also been recorded (VanArsdel et al., 1956). Line and sex differences have been observed. It was necessary to develop proper leads for taking electrocardiogram (EKG) recordings and to establish normal values with which deviations could be compared (VanArsdel et al., 1959, 1960a,b; Krueger and Van Arsdel, 1959; Krueger et al., 1960). In all cases in which an animal was diagnosed from the EKG and later autopsied, the diagnoses from the EKG records were correct (VanArsdel et al., 1957). Studies by VanArsdel and Bogart (1961) indicate that abnormalities in heart function occur at a fairly high frequency and are responsible for poor performance and sudden, otherwise unexplained deaths. Heart rates also are influenced by diet, with higher heart rates occurring when animals are on a high feed intake.

Higher heart rates and body temperatures are associated with more rapid rates of gain (Williams et al., 1953, 1954). It appears that growth increases metabolic rate and thus heart rate and body temperature. In selecting for more rapid growth there has been an increase in striated muscle but not in heart muscle; therefore, rapidly gaining cattle may be approaching a state of heart stress because there may not be sufficient time for cardiac tissue rest.

INHERITED LETHALS AND ABNORMALITIES

Chronic bloating is highly heritable (65%), as shown by mating bloaters to bloaters and to close relatives (Bogart, 1962). Eye cancer (Figure 7, a and b) occurs at a relatively high frequency in Hereford cattle (4-5%) among cows four years of age or older in areas where bright sunlight, dust, and pollens are abundant, and its frequency of occurrence
is much higher in animals lacking pigment about the eye. Breeds having pigment about the eyes have less than one percent incidence of eye cancer. Susceptibility to cancer appears to be inherited, but whether or not cancer develops depends upon the presence of eye-irritating agents (dust, pollen, and bright sunlight). Eye irritation is much greater in animals having no pigment about the eye (Guilbert et al., 1948; Woodward and Knapp, 1950). It appears that eye cancer is under genetic control, since heritability estimates of 0.17 to 0.30 have been obtained (Blackwell et al., 1956).

Double cervix was first reported by Sittman and others (1961) as a sex-limited abnormality, and it may be caused by a simple autosomal recessive in the homozygous condition (Sittman, 1963). A double cervix does not appear to reduce conception rate.

Woodward and Quesenberry (1956) reported 93 cases of vaginal or uterine prolapse out of 7,859 births, and Holland and Knox (1967) found that 27 out of 150 cows removed from the purebred herd over a period of 30 years were culled because of vaginal prolapse. They found no vaginal prolapse in 400 grade cows on semi-desert range that were removed from the herd, even though the two herds were genetically related. They estimated the heritability of vaginal prolapse at 0.57.

Semihairlessness has been described as nonlethal and is inherited as an autosomal recessive (Kidwell and Guilbert, 1950).

Stillbirths have been reported in most every herd and Woodward and Clark (1959) gave the frequency among 8,857 births as 3.6 percent. They report that male calves, twins, more highly inbred calves, and those born by posterior presentation had higher deaths.
Spastic calves were reported by Stonaker (1958a) to be of genetic origin but the exact mode of inheritance was not determined. Wry calves (Gregory, 1954) appear to be of two types; one is associated with dwarfism and the other, which has been observed only in Herefords, is not associated with dwarfism. The frequency of the latter type may be as high as 15 percent and it appears that nutrition is involved as a causative factor. The latter group of wry calves are also called "crooked calves."

Albinism (Figure 8) causes an absence of pigmentation in cattle, resulting in photophobia when they are in bright sunlight (Hafez et al., 1958; O'Mary and Ensminger, 1959). Breeding results suggest albinism is due to autosomal recessive genes in the homozygous condition. Survival of albinos is low because of hemorrhage following castration (Ament and O'Mary, 1963). A chemical and histological study showed that some melanin is present in the hairs of albino cattle, which means they are extreme dilutes rather than true albinos (O'Mary and Levinsky, 1964). The leucocytes of albinos contain abnormal granules similar to those found in Aleutian blue mink. These granules are also typical of the Chediak Higashi Syndrome in man.

Figure 8. Albino cow and calf. Note sensitivity to bright sunlight exhibited by the calf. (Courtesy Ralph Bogart; picture taken at Washington State University.)
Hydrocephalus (Figure 9) is characterized by fluid accumulation in the third and lateral ventricles of the brain (Krueger et al., 1955). It is sometimes associated with dwarfism (Pahnish et al., 1955a,c; Blackwell et al., 1959; Tyler et al., 1959a,b), but it also occurs in non-dwarf calves.

Cardiac ventricular septal defects observed in Hereford cattle (Bellings, 1962) is genetically controlled but the exact mode of inheritance is not established. Present evidence indicates it is an autosomal recessive. VanArsdel and Bogart (1964) described the W-P-W Syndrome in a Hereford cow. They also described a heart abnormality, but breeding the bull so afflicted to related cows failed to result in calves with the heart abnormality (VanArsdel and Bogart, 1964). Research at the Oregon Station (Krueger and Van Arsdel, 1959; Van Arsdel et al., 1959; Krueger et al., 1960) has established the normal EKG pattern, and variations indicate that the poor-doing of some animals and the sudden death of others may be the result of abnormal heart function.

Double muscling (Figure 10) in Angus cattle is characterized by heavy muscling of the round in the heterozygote but by shallow body and...
abnormal pelvic shape in the homozygotes. It appears to be caused by an incompletely dominant gene (Rollins, Julian, and Carroll, 1968). There is generalized muscle hypertrophy in double-muscled animals.

Dwarfism has received much attention because of its great economic importance to the beef cattle industry. There are two major kinds of dwarfs—the short-headed or snorter kind is called brachycephalic, while the long-headed kind is the dolichocephalic dwarf. Many of the early studies were concerned with the short-headed or snorter dwarf. Symptoms of the condition were well described from superficial phenotypic observations (Gregory et al., 1951c; Lindley, 1951; Pahnish et al., 1955b) as protrusion of the tongue and eyes, some lack of coordination, short cannon bones, prominent forehead, enlarged abdomen, labored respiration, slow growth, high susceptibility to bloat, and high mortality. This type of dwarf was reported to be caused by an autosomal recessive gene (Gregory et al., 1953; Pahnish, 1955a). Gregory and Carroll (1956) reported that the gene existed in other breeds besides the Hereford where it was first reported. Dwarf animals can reproduce, but fertility is low and calving difficulties occur (Gregory et al., 1951c; Lindley, 1951; Pahnish et al., 1955a,b). Dwarf bulls have difficulty in serving cows and dwarf cows are low in fertility and have calving problems that may require delivery by caesarean operation (Pahnish et al., 1955b). Kidwell (1951) reported probability figures for detecting the dwarf gene in normal animals, and Pahnish and others (1955c) outlined alternative methods by which breeders could detect dwarfism by progeny testing.

Methods were sought for differentiating the dwarf carrier from the homozygous normal animal. The first method was the recording of head profiles (Gregory and Brown, 1952; Gregory et al., 1952, 1953), since it was known that dwarf animals had a bulging forehead and it was suspected that carriers of the dwarf gene might also exhibit some bulging of the forehead. This method was found to be reasonably accurate for horned Hereford bulls two years or more of age. Stratton and others (1956) studied head forms earlier and found that profiles taken at six months were not indicative of the subsequent profile. Profile records were not accurate for females (Gregory et al., 1952, 1953); therefore, Schoonover and Stratton (1954) tried to develop a pegboard for obtaining profiles on females. This did not prove successful. Stonaker (1954, 1958a) reported on a dwarf type obtained by inter se matings of comprest cattle. Many of these dwarf calves had crooked legs. Stonaker was of the opinion that this dwarf condition was due to an incompletely dominant gene.

Gregory (1955) reported on both long and short-headed dwarfs and crosses between them that gave a comprest type which he termed "synthetic comprest." He concluded that there was one major recessive
Figure 10. Double muscling in cattle. Top photo, opposite page: Rear of normal animal (left) and double muscled animal (right). Note enlarged muscles with vertical crease in double muscled animal. Lower photo, opposite page: Carcasses showing round of normal animal (left) and double muscled animal (right). Above: Loin-eye areas of normal animal (left) and double muscled animal. Note greater amount of lean and larger loin-eye area in double muscled carcass. (Courtesy Wade Rollins, University of California.)

gene for dwarfism, with modifying genes affecting dwarf expression. Julian and others (1959) reported four dwarf types—the long-headed (Figure 11), the short-headed (Figure 12), an intermediate, and the comprest (Figure 13). In addition to this list, Dexter-type “bulldog” calves (Figure 14) have been produced by long-headed dwarfs mated to a Dexter bull (Gregory et al., 1960). Although Hafez and others (1958) reported albinism and dwarfism in the same animal, it is likely that these are two separate and independent traits. Gregory and others (1957) questioned the reliability of the progeny test for detecting dwarf carriers because of the influence of modifying genes on the dwarf gene.

Early endocrine studies indicated a thyrotropic hormone deficiency in the pituitary glands of dwarf calves (Carroll et al., 1951) but gonadotropic and growth hormone levels were normal (Carroll and Gregory, 1962).
Figure 11. Long-headed dwarf. (Courtesy P. W. Gregory, University of California.)

Figure 12. Short-headed dwarf (right) and normal animal (left). (Courtesy Ralph Bogart, Oregon State University.)

Chemical and hematological studies showed that the short-headed dwarf is not a thyroid-deficient cretin. Most of the blood values were...
normal except for lymphocytes and neutrophils (Cornelius et al., 1956; Hafez et al., 1959). There were subnormal values for hemoglobin, hemat-
crit, and white cell counts but blood chemical constituents were normal. Urinary excretion of greater quantities of glutamic acid by dwarf calves was reported (Asplund et al., 1956), and chondroitin sulfate-A was found in the urine of short-headed dwarfs (Tyler et al., 1962). This is the main urinary polysaccharide found in the urine of achondroplastic human dwarfs. Chondroitin sulfate-B and heparitin were not found in the urine of dwarf calves, which shows that dwarfism is not homologous with Hurler's Syndrome (gargolism) in humans.

Cytological studies (Leuchtenberger et al., 1956) showed that DNA content of sperm from dwarf bulls was more variable than that found in sperm of normal bulls, but this variability in DNA was not due to differences in chromosome number.

Tyler and others (1957) observed disproportionalities in the appendicular skeleton of the short-headed dwarf. The disproportionalities were due to short diaphyses combined with normal epiphyseal lengths and bone widths. The most severe disproportionalities occurred in animals up to two months of age. It was concluded that hypoplastic achondroplasia is the dwarfing process and this process is indicated in utero.

Premature fusion of the sphenoid synchondrosis in short-headed dwarfs was reported (Julian et al., 1957). While fusion in phenotypically normal animals was found to begin at about 24 months of age and terminate by 36 months of age, partial fusion in most dwarfs was apparent at 1 to 18 days of age. Fusion was complete in all dwarfs examined at 5.5 months of age or older.

Tyler and others (1959a,b) reported that two projections into the cranial cavity were common in achondroplastic dwarfs, although a lower incidence was observed also in non-achondroplastic animals. The wing of the orbitosphenoid projected medially and dorsally into the cranial cavity, and the posterior intraoccipital synchondrosis projected medially and anteriorly into the cranial cavity.

Investigation to determine the nature of the articulations of the lumbar vertebrae were conducted by Gregory and others (1961b). The change in articular pattern was reported to be a function of age, with the arthrodial type progressing to the trochlear type. Only the arthrodial type was found in animals up to 122 days of age. A transition from the arthrodial type to the trochlear type occurred between the age of 4 and 16 months, with the change starting at the anterior end of the lumbar region and progressing posteriorly. The type of articulation was affected little, if any, by breed, sex, or castration.

4 Arthrodial refers to a gliding motion, while trochlear refers to a pulley type of movement.
Tyler and others (1961) formulated three metacarpal indexes which they considered useful in diagnosing the brachycephalic dwarf type. The indexes were reported to be relatively independent of age or sex, and less than 3.0 percent of the index values for dwarfs overlapped the values for phenotypically normal controls. The ranges in metacarpal index values were as follows:

<table>
<thead>
<tr>
<th></th>
<th>Total length divided by diaphyseal length</th>
<th>Total length divided by diaphyseal diameter</th>
<th>Diaphyseal length divided by diaphyseal diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brachycephalic dwarfs</td>
<td>1.21 to 1.29</td>
<td>3.3 to 3.4</td>
<td>2.7 to 3.8</td>
</tr>
<tr>
<td>Control cattle</td>
<td>1.14 to 1.19</td>
<td>4.7 to 7.5</td>
<td>4.1 to 6.4</td>
</tr>
</tbody>
</table>

The influence of achondroplasia on the width and cell content of distal, metacarpal, and epiphysial lines was investigated by Ticer and others (1961). The zone of resting cartilage in dwarf specimens was narrower and contained fewer cells than did the same zone in the controls (P < .01). The zone of proliferation in dwarf animals was relatively wider and contained relatively more cells than did this zone in control stock (P < .01).

Gregory and others (1961a) used anatomical diagnostic characteristics to compare short-headed dwarfs from several types of compound matings with short-headed dwarfs produced by control parents of normal size. They concluded that short-headed dwarfs by compound parents and by control parents were identical biologically and genetically. Diagnostic characteristics used included projections into the cranial cavity (Tyler et al., 1959a,b) fusion time of the sphenoid-occipital synchondrosis (Julian et al., 1957), and the three metacarpal indexes previously discussed (Tyler et al., 1961).

Gregory, Julian, and Tyler (1963, 1964) progeny tested three Hereford bulls for achondroplastic dwarfism using their metacarpal indices and the time of fusion of the sphenoid-occipital synchondrosis for diagnosis. The results showed that classification of test progeny for achondroplastic dwarfism by visual inspection is ineffective and proved that the accepted hypothesis of inheritance of achondroplasia is untenable. They postulated that alleles segregating at two or more loci are capable of producing the same type of dwarf and that several mutant types are components of the achondroplastic complex. They feel that selection for short, compact cattle may have forced a directional evolution which resulted in several forms of achondroplastic deterioration. Perhaps the most important factor...
in reducing the frequency of dwarfism in beef cattle has been selection for longer bodied, faster gaining animals that are larger at maturity.

In studies of the achondroplastic mutants, some of the segregates resembled the commercial Dexters. Some of these were mated to registered Dexters to determine if they would produce “bulldog” lethals and Kerry types. From the short-headed dwarf x Dexter, Dexter type and “bull-dog” types were produced and from comprest x Dexter, Kerry, Dexter, and other unclassified segregates were produced (Gregory, Tyler, and Julian, 1966). Their evidence indicates that the major achondroplastic-conditioning gene is recessive for all achondroplastic types and that interaction of alleles at two other loci that are independent modify the major gene to simulate its action as dominant in certain cases.

Mayes and others (1964) reported that urinary mucopolysaccharide excretion studies with dwarf cattle and patients with Hurler’s disease show that the two conditions are quite different.

BEHAVIORAL STUDIES

Although it is recognized that certain behavioral traits are important and should be included in a selection program, not much has been done on behavioral studies. Ray and Roubicek (1969) studied feedlot behavior under hot and moderate temperatures. They observed that cattle tended to eat early in the morning and late in the afternoon and to lie down much of the other time. Animals in the moderate temperature ate more frequently during the middle of the day than those under high temperatures, while animals under the high temperatures consumed water more frequently. During the high temperature (summer), all steers moved under shade at 6 to 7 a.m. and remained there until 5 to 7 p.m. Under moderate temperature (winter), cattle used the shade only from 10 a.m. to 3 p.m. and only about half of them were under shade at any one time.

Wagnon and others (1966) compared Angus, Hereford, and Short-horn cows for social dominance. The Angus showed the strongest social dominance, followed by Shorthorns, and the Herefords showed the least. There was a positive correlation of size with social dominance within breed, but the Angus breed was the smallest and showed the most social dominance.

Roubicek (1965) studied cattle with and without water and shade, and without shade. Body temperatures rose from 101°F to 103°F by noon when animals were in the sun. Animals allowed water maintained 102°F even though the air temperature rose to 104.5°F by 5 p.m., while body temperature of those without water increased to 105.5°F. Thus, water is essential under high temperatures and lack of it for two days might lead to death.
Laboratory animals are often used for developing or testing concepts before these methodologies are used with farm animals or as assay animals for determining concentrations of hormones in tissues of farm animals.

The Oregon Station crossed four strains of mice, each strain having been selected differently in its development as a closed population. One strain had a higher than normal vitamin (biotin and/or folic acid) requirement but a low thyroid secretion level while another strain was somewhat hyperthyroid. Crosses of females of the former strain with males of the latter strain gave striking results. The young had a high metabolic rate and a high vitamin need, but their mothers could not supply them with the needed vitamin. Practically every young in this cross died or did very poorly (Mason et al., 1956a,b) unless biotin and folic acid was given in excess to the mother or the young.

Rollins and Cole (1952) found that variability in ovary weights of rats declined with inbreeding, indicating that 80 to 85 percent of the variability in ovary weights was due to inheritance; consequently, these rats gave five to seven times the precision in bioassays as random-bred rats.

Kidwell and others (1962) reported that selecting rats for 70-day weights under two levels of feeding regulated by inclusion of roughage in the diet increased 28- and 70-day weights and litter size but not significantly. There appeared to be interactions of selection, time weight was taken, and levels of feeding in repeatability. Bailey and Weeth (1963) found heritability of 70-day weight to be 0.20 in the line on concentrate and 0.16 in the line on roughage feeding. Since large numbers of rats were involved in the study, these heritability estimates were significantly different even though they were similar. Subsequently, Bailey and others (1970) found evidence of a genotype x environment interaction within sire lines. In each of the four lines, the rank of sires varied according to the nutritional regimen under which progeny were evaluated. However, effects of sire line x nutritional regimen interaction on postweaning growth rate, feed conversion, and carcass components were negligible. Heritability of postweaning gain was higher in the lines selected under concentrate feeding than for those selected under roughage feeding. Sires from lines selected under concentrate feeding were superior to those selected under roughage feeding when mated to random-bred females.

Carroll and Gregory (1962) found that pituitary material from dwarf cattle stimulated growth in Snell dwarf mice as effectively as pituitary from normal cattle, which indicated that dwarf cattle are not the result of hypo-growth hormone in the pituitary.
Since it is known that selection is effective only when genetic variation exists and that radiation causes genetic variation, it was important to investigate the possibility of enhancing selection progress by creating genetic variation. Womack and Bogart (1968) investigated the effects of radiation in mice on selection progress, using 0, 25, 50, and 100 r x-irradiation. Although more genetic variability existed in the irradiated lines, selection was not effective because irradiation reduced fertility to such an extent that little or no selection could be applied. An investigation on the reduced fertility showed that female mice that received 50 or 100 r of x-irradiation were sterilized by the irradiation and did not recover. Fertility was normal or above normal if the female conceived during the first estrus following irradiation but was not normal subsequently. Male mice apparently recovered from x-irradiation damage to the testicle in contrast to continued sterility in females (Womack and Bogart, 1969).

Hunt and Bogart (1964) put irradiated and non-irradiated ova of rabbits into irradiated and non-irradiated uteri. The uterus could tolerate much higher doses of x-irradiation than the two-celled ovum. An ovum that received 61.2 rads in a uterus receiving 250 rads of x-irradiation had a reasonable chance for development, but if either an increase of 30 rads to the ovum or an increase of 15 rads to the uterus were given, 100 percent of the ova died.

Jones (1971) studied x-irradiation of hamster ova. Great chromosomal damage developing from x-irradiated ova was found when the embryos were examined early in development, but no chromosomal damage developing from x-irradiated ova was found in fetuses or in animals delivered at term. However, there were many abnormal young born to mothers bearing young that were irradiated as ova. It appears that cells having damaged chromosomes die and do not reproduce themselves in the mitotic process. These cells probably are of great importance in developmental processes and their loss causes abnormalities of development. These results would lead one to believe that the likelihood of finding chromosomal abnormalities in newborn farm animals that are abnormal is not great, but that a failure to find chromosomal abnormalities is not proof that original abnormalities of the chromosomes are not the cause of abnormality in newborn animals.

APPLICATION OF RESEARCH FINDINGS

Heritability estimates have been established for the most important commercial traits. These estimates for the most part are positive and, if applied effectively, should lead to a constant rate of improvement in the desired characteristics (Figure 15).
Growth of calves has the same linear expression during different periods when the environment is constant. Under stress conditions, growth during one period may be negatively related to growth during other periods.

Heavy calves at birth generally gain more rapidly than light calves. Year effects have been rather large for most of the production traits. This shows that environmental factors have a significant effect on performance of cattle. This means that difficulties will be encountered in comparing calves born in different years unless one has some method of considering the differences in the years the calves were born. At the present time, it appears best to keep about the same percentage of replacement animals each year rather than keeping more during a good year when records look good and culling most of the calves during adverse years when records are low.

Selection pressure can be applied more strongly to bulls than to females; therefore, great attention should be given to bulls in a selection program. In general, selection is more effective in a moderately desirable environment than in an austere one because under severely adverse environments, one may not be selecting for performance but for ability to withstand the adverse environment.
Weight at 15 to 18 months of age appears to be one of the most important characteristics in beef cattle production because calves must have a high rate of gain during both the preweaning and the postweaning period. Calves which are large at 15 to 18 months of age will be efficient in converting feed into gain and will likely breed and produce a heavy calf.

Postweaning rate of gain, efficiency of gain, and carcass leanness are highly heritable, while heritabilities of fertility and its components are low and heritability of milking ability (suckling gains) is low to moderate. These heritability estimates, coupled with the marked depressing effect of inbreeding on fertility and weaning weights and the high heterotic responses from crossbreeding for traits associated with calf-producing ability, again suggest that crossbreeding of highly selected stocks will be most effective. Selection for more rapid gains will bring about greater efficiency in feed use and larger adult body size. There is not much association between preweaning and postweaning gains; therefore, selection methods and breeding systems must be geared at improving both of these traits since selection for one will not improve the other. Selection for conformation does not cause changes in rate and efficiency of gains. Feed consumption is moderately heritable, and it influences feed efficiency to a considerable extent.

Mature cows and larger cows of comparable age produce heavier calves at weaning than younger or smaller cows. In selecting calves at weaning, one would be advised to adjust weaning weights of calves for age of dam to prevent penalizing calves from younger cows. Adjusting weaning weight of calves for differences in sizes of dams may or may not be desirable. Making adjustments of calf weaning weight for size of dam would imply that a smaller calf from a smaller dam is as desirable as a larger calf from a larger dam. The studies so far indicate that conventional cattle grow more rapidly and economically and produce carcasses with more lean and less fat than crossbred cattle if they are fed to comparable weights. The conventional cattle also have a longer productive life.

There appear to be some negative genetic relations between milking ability and growth rate. This suggests that no one breed may possess all desirable characteristics and that selection within each breed for a trait or traits to combine with other breeds in a crossbreeding program may become the most effective method of beef production.

Bull calves grow more rapidly than steers and steers grow more rapidly than heifers. The difference in growth between the sexes is more evident under good feed conditions than under adverse conditions. Some producers may find it profitable to produce bull beef because carcasses
from bulls slaughtered at young ages (up to 15 months) are tender and contain more lean and less fat than steer carcasses. Bulls eat no more than heifers at comparable weights but they gain more rapidly; therefore, bulls are much more efficient in feed use than heifers.

Many of the carcass traits are highly heritable but they cannot be measured in the live animal and this prevents selection for them. The progeny test is perhaps the most effective method now available for selecting for carcass desirability. Rate and efficiency of gains are positively related to lean and negatively related to fat percentages of the carcass. Most of the scores and measurements of the live animal show low predictive values for carcass merit. It is possible to predict carcass value from studies of certain cuts from the carcass. Inbreeding tends to reduce the amount of lean and increase the amount of fat in carcass of a constant weight. Methods such as biopsies are needed so that carcass evaluations can be made on live animals. Also, nuclei numbers in muscle from biopsies as well as fat and lean ratios might be important both as predictors of subsequent carcass merit and as evaluators of carcass merit at a slaughter weight. Ultrasonic measures of fat and lean and the use of photogrammetry may help to predict wholesale cut-out values in live animals.

Inbreeding tends to depress production traits, with the more highly heritable traits of rate and efficiency of gains and body size being depressed less severely than the less highly heritable traits of fertility and preweaning gains. There is also greater mortality, particularly at birth, as well as a greater frequency of abnormalities as inbreeding increases. In a large closed population where several sires are used selection can be effective in preventing the depressing effect of inbreeding even for the less highly heritable traits, but selection is much more effective in preventing inbreeding depression in the highly heritable traits.

Several abnormalities of the reproductive tract or germ cells have been reported and many of these are inherited as simple autosomal recessives. Some are sex-limited. Generally, the heritability of fertility is low, even zero in some cases, which shows that direct selection for fertility is relatively ineffective. There are some indications that size and shape of the pelvic canal can be measured in the live animal and animals that are likely to have calving problems can be culled. Under sparse range conditions, young cows may fail to conceive because they are not obtaining sufficient nutrients to lactate, grow, and reproduce. Feed supplementation did not increase conception among young cows on sparse range, but early weaning of calves to remove the lactation drain materially increased conception rate. More calving problems occur when young cows are bred to bulls of large breeds, particularly in the delivery of bull calves. If bulls of large breeds are used, they should be bred to more mature cows. Cross-
bred bulls and heifers reach sexual maturity at younger ages than straight-breds. The use of hormones to synchronize estrus and to superovulate cows for the production of twins or for ova transfer is in the experimental stage at present, but the prospects for developments are promising.

The greatest effects from crossbreeding are the reduction in mortality at birth, increased fertility of breeding animals, increased milking ability of cows, and the ability of animals to withstand adversities. Heterotic effects are evident in all production traits but are generally greater for traits concerned with cow productivity. Conservative estimates would indicate a 5 to 10 percent advantage in overall production from a well-planned crossbreeding program. The breeds to use in a crossbreeding program need careful consideration because the best combinations for obtaining maximum heterotic effects depend on feed conditions, management practices, and marketing situations.

A crossbreeding program could be adopted with little or no increase in costs for bulls, assuming that Angus, Shorthorn, and perhaps some other breeds of bulls equal in quality to Herefords could be purchased at about the same price. Several approaches to adoption of crossbreeding could be made.

1. **Gradual.** Replace 20 percent of the bull inventory each year with bulls of two other breeds. The culling and cow replacement program would continue as it would without crossbreeding. This gradual rate of adoption of crossbreeding would result in about a 17 percent increase in net ranch income before taxes, averaged through the period of adoption. Most medium to small operations probably replace more than 20 percent of bull inventory each year.

2. **Moderate.** Replace 40 percent of the bull inventory each year by bulls of two other breeds. This approach increased net ranch income before taxes by about 18 percent through the period of adoption. Cow replacement program was maintained on a normal basis in this strategy also.

3. **Rapid.** Replace 100 percent of the bull inventory at the start of crossbreeding program but maintain a normal cow replacement program. This results in a 19 percent increase in net ranch income averaged through the period of adoption.

4. **Very rapid.** Replace 100 percent of the bull inventory and replace the straightbred cow herd with crossbred cows as rapidly as possible. This approach to crossbreeding adoption resulted in an increase of 18.6 percent in net ranch income before taxes.

All approaches result in a complete conversion of cow herd to crossbreds and to sale of second-cross animals. Consequently, all yield the same net income increase, 23 percent, after the program is fully adopted.
The very rapid rate of adoption shows relatively little advantage in turns as compared with the gradual rate of adoption represented by replacement of 20 percent of the bulls each year and the normal cow replacement. Moderate or very rapid adoption shows slight advantage over gradual adoption in average returns through the adoption period, and the three approaches would be equivalent at the completion of adoption. Gradual bull and normal cow replacement allows for evaluation of the practice before any extreme commitment is made. In effect, it permits a ranch operator to revoke the practice and return to a straight-breeding operation within the first four or five years with negligible ill effects on the ranch operation, the composition of the cow herd, or net returns. The very rapid rate of bull and cow replacement would have disadvantages if revoked. Costs associated with the liquidation of the undepreciated portion of the inventory (bull), which are not great when distributed over 15 years, must be absorbed immediately if the practice is revoked. There would be a second inventory of bulls, and additional costs would be encountered in liquidating the undepreciated portions of that inventory. A need for additional pasture fencing, if any additional costs are required, occurs in about the fourth and seventh years of the rapid adoption program rather than in the sixth and eleventh years of the gradual replacement program.

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