

GENETIC AND ENVIRONMENTAL FACTORS INFLUENCING APPETITE
IN BEEF CATTLE AND THE RELATION OF APPETITE
TO RATE AND EFFICIENCY OF GAIN

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INTRODUCTION

From the standpoint of efficiency of feed conversion and diversity of products yielded, beef cattle are at a decided disadvantage compared to the other classes of livestock. The primary useful product derived from beef cattle is meat, and as a meat-producing animal the beef cow cannot compare with the chicken or with swine in efficiency of feed conversion. The beef animal is not only less efficient in converting feed into meat, but the year-round maintenance cost of the cow per pound of meat produced by her calf is extremely high compared to animals such as poultry and swine. The gross efficiency of meat production by beef cattle is about 5 to 10 per cent as compared to an efficiency of about 33 per cent for milk production and 16 per cent for egg production. When one adds to this disadvantage in efficiency the fact that sheep produce two useful products, namely wool and meat, then it can be seen that beef cattle would be in a particularly poor bargaining position for available grain as compared to the other classes of livestock.

The disadvantages enumerated above are offset by the fact that beef cattle can convert an unedible commodity,

so far as man is concerned, into food for human consumption. It is on this basis that the production of beef cattle must ultimately be justified. The high concentrate feeding practices presently employed in beef cattle production will persist only as long as there is no serious competition from other more efficient classes of livestock and from humans for these grains.

There are indications in the literature that a considerable variation exists among dairy cattle with respect to roughage intake. There is also work, however, that indicates that very little variation exists for roughage intake in sheep except for that due to differences in body weight. It is of interest, therefore, to determine if beef cattle exhibit real differences in their willingness to consume a high roughage diet at given body weights. A determination of the influence of various environmental and genetic factors upon feed intake is also in order. It is likewise desirable to examine the relationships between feed consumption, rate of gain, and feed efficiency.

The present study proposes to determine the role of appetite (as measured by feed intake) upon growth and feed efficiency of beef cattle during a constant-weight feeding period, using a ration that is constant in proportion of protein and energy. The objectives of this study are to:

1. determine the relationship between body size and feed intake as body weight changes from 500 to 800 pounds.
2. ascertain changes in the ratio of nutrient intake per unit of body weight as weight increases.
3. determine the differences in appetite between males and females and the extent to which this difference is reflected in the rate of gain and feed efficiency for the two sexes.
4. determine what environmental and genetic factors influence feed intake, rate of gain and feed efficiency.
5. examine the relationship between feed intake, rate of gain, and feed efficiency.
6. determine to what extent daily feed intake is hereditary and whether or not it should be used as a criterion for selection in a breeding program.

If heritable variations do exist for feed intake, then it is possible that breeding for an increased roughage appetite would be economically sound in the years to come.

LITERATURE

According to Webster, appetite is an inherent or habitual desire or propensity for some personal gratification of mind or body. It is a craving of, a desire for, or relish of, food or drink. Food acceptance may be measured by (1) the method of immediate choice, (2) the rate of ingestion, and (3) the amount of intake. Under a nutritional regime in which the ration offered is of the same composition for all individuals, the food intake under ad libitum feeding conditions is a measure of appetite.

It has been suggested (24) that six variables are involved in the regulation of feed intake, namely: (1) environmental temperature, (2) the integrity of several hypothalamic structures, (3) palatal stimuli and gastrointestinal distension, (4) emotional and conditional responses, (5) circulating metabolites, and (6) genetically determined metabolic pathways.

Environmental temperature has been shown to have a marked effect on appetite, as measured in terms of feed intake, with subsequent effect on growth and productivity. Temperatures above 80°F. have been found to reduce TDN intake and lower productivity (16, 21). There is also evidence that the temperature range is of importance in the growth rate of animals. Generally speaking, where

seasonal temperatures are less variable growth rate is also less variable.

It has been demonstrated that an area in the hypothalamus is specifically concerned with the regulation of food intake. When the middle portion of this region was experimentally damaged in rats, feed intake increased and the animals became obese. However, lesions in the lateral portion caused the animals to stop eating, which resulted in starvation (19). A "glucostatic" theory has been advanced (29) which postulates that the available carbohydrate supply of the body exerts a regulatory influence on food intake via hypothalamic glucoreceptors; that is, the urge to eat increases as carbohydrate stores diminish. Other investigators (6, 30) have found that the level of blood glucose had no effect upon short term appetite in sheep and in dairy cattle. Injections of isotonic glucose solution into the medial area of the hypothalamus of rats in which the eating desire had been increased by injection of procaine failed to bring about a change in the eating pattern. Repeated injections did not suppress the vigorous eating of the rat (19). On the basis of the results obtained from manipulation of blood glucose level, it would seem that the glucostatic theory does not adequately explain the regulation of food intake, particularly in ruminants.

Palatability of feeds has long been believed to be of importance in determining the readiness with which the animal will consume feed. Total quantity of food ingested is influenced by palatability. It seems, however, that the palatability of a food in most cases is related to its energy content so that the difference between the total amount ingested of several feeds may be more influenced by their relative energy levels than by their comparative palatabilities. Blaxter et al. (3) have concluded that palatability as such has practically nothing to do with the voluntary consumption of long fodders. He found that intake was related to the digestibility and rate of passage of foods, which are attributes hardly consonant with acceptability of foods to the palate or taste. Crampton (9) agrees with this viewpoint and states that the extent of the voluntary consumption of a forage is limited primarily by rate of digestion of its cellulose and hemicellulose rather than by contained nutrients or the completeness of their utilization. The dependency of intake upon rate of passage indicates that gastrointestinal distension is a major factor influencing food intake. Hence, Blaxter reached the conclusion that within the limits of the fodder quality studied, the amount of food eaten by sheep is determined by the capacity of their digestive tracts; consequently, physical rather than physiological

factors regulate appetite.

It appears that the energy level of the diet influences the amount of intake (35). Chicks fed rations diluted with cellulose or kaolin attempted to compensate for reduced nutrient concentration by increased food intake.

There is evidence that individual differences in food intake may be due partially to the inherent willingness of the animal to take in feed. Some cases have been reported which have emphasized gene-determined individual differences in ability to select food wisely. Dove (12) reported that some chicks, given the same choice among several foods, appear to select and balance their diet wisely, while others were less wise in their choice. These differences were indicated by growth and reproduction. The same ability to balance the diet has been observed in dairy cattle, laboratory rats, and other animals (41, p. 213). The term "aggridant type" has been coined by Dove (13) to designate the nutritionally superior type of individual. The aggridant type is characterized by superiority in physical form, size, rate or reproduction, longevity, efficiency in the use of foods and consistency in reaction. Dove prepared rations that were consistent with those selected by the aggridant type and reported as much as 30 per cent increase in growth above the average by feeding all the individuals this ration. These results

suggest a relationship between the inherent growth capacity of an animal and its ability to choose food wisely.

Work with dairy cattle (37) has shown that highly significant differences exist among individual cows for roughage intake. Differences in dry matter intake were present after adjusting for differences in milk production, body weight, and daily changes in body weight. Only 25 per cent of the differences were associated with these variables while 75 per cent was attributed to individual differences between cows. This information indicates that some cows eat until they are partially or moderately filled, while others keep eating until they are gorged or filled to full capacity. The cows showed a tendency to maintain their intake rank on all kinds of roughage.

Efficiency of milk production is largely independent of body size (37). The increase in production and the increase in feed intake associated with increase in body size are about the same. There are apparently only small differences in the way in which roughages are digested and the efficiency with which the absorbed nutrients are utilized. There has been reported (37) an average coefficient of variation of only 2.2 per cent for 300 different digestion trials involving 90 to 100 animals. Nelms, Price and Bogart found none of the digestion coefficients studied related to rate and efficiency of gains (31, p. 217).

The authors indicate, however, that the absence of such correlation could be due to lack of adequate techniques in determining digestibility. The heritability of digestibility and of efficiency of use of digested nutrients would thus be quite low, whereas the individual differences in roughage appetite assume a great deal of importance.

In an experiment involving Shorthorn, Brahman, and Shorthorn x Brahman crosses, Hargrove et al. (17) found that appetite was highest in crossbred calves, followed in turn by Shorthorn and Brahman. The authors do not state, however, whether corrections were made for weight and age of the calves. Some differences in weight might be expected between breeds if all were the same age. The crossbred calves also exhibited the most rapid rate of gain. The Brahman calves gained somewhat less rapidly than the crossbreds, while the Shorthorns made the least amount of gain per day when all three groups were full-fed.

The yellow mouse has been used to study hereditary obesity and efficiency of food utilization. Yellow coat color in the mouse is produced by a dominant autosomal gene in the heterozygous condition. Crosses of yellow with non-yellow mice give approximately equal numbers of yellow and non-yellow progeny within each sex. This mating plan was carried out by Dickerson and Gowen (11). They mated yellow males of a highly inbred stock with

albino females of another highly inbred line. The yellow and black littermates of the same sex differed presumably only in the one chromosome which carried the "yellow" gene. Sets of yellow and black littermates were compared within each sex and growth period. The evidence from this study indicates that the "yellow" gene in mice increases the food intake and reduces energy expended, especially for activity, and thereby reduces food requirements per unit of gain and produces obesity.

Blaxter (3) has stated the opinion that animal-to-animal variation in voluntary intake is small and that the possibility of breeding sheep for increased food intake is limited by a lack of real variation among animals. Other work, however, indicates that gene-determined differences in food intake do exist among individuals. According to Trimberger (37), preliminary calculations indicate a difference of 10 per cent in roughage intake among daughters from different sires in dairy cattle. It is probable, therefore, that it would be economically sound to breed cattle for increased appetite and, consequently, increased roughage intake with resultant increased growth on this type of ration.

The response of body weight changes to sex hormones and gonadectomy varies according to animal species and conditions. It has been found that castration causes

considerable increase in adiposity in the fowl, but decreases body weight increases of lambs and goats below that of comparable intact animals. Castration has been found to cause increased body weight and food intake in female rats, but not in males. Conversely, it has been shown that in fowls small doses of diethylstilbestrol depressed basal metabolic rate; larger doses also increased food intake (28, p. 488-489). Data from the Illinois Experiment Station have shown that when both bred and open heifers were fed at the same rate, the bred animals showed a greater desire for more feed than the open heifers. It has been postulated that male animals may consume more food than females, even when adjustments are made for weight (36, p. 275). Work at the Oregon Experiment Station indicates that this is not the case in beef cattle. Ampy et al. (1) have found that there is no significant difference in daily feed intake between males and females at equal weights for animals on feed from 500 to 800 pounds. The females were, however, older than males at any given weight since their rate of gain was less rapid. Rate of gain per day decreased more with increasing age in females than in males. Likewise, feed required per unit of gain increased more noticeably in females than in males.

The efficiency of feed utilization is influenced by the level of feed intake. Generally speaking, the greater

the feed intake the lower the feed utilization and the less the net energy per unit feed consumption (7, p. 90). It is usually assumed, however, that the greater the food consumption, the more rapid is the growth of the individual. Gains are thus more economical because of some saving in maintenance costs.

In pigs fed ad libitum at 4, 3, and 2 pounds feed per 100 pounds body weight, it has been observed that while the growth rate decreased with decreasing feed allowance, the weight gain per unit feed consumed increased (7, p. 91).

In three trials, weanling steers from one experimental cow herd and sired by closely related bulls, were individually fed to make 400 pounds total feedlot gain either (1) rapidly, (2) moderately, (3) rapidly for 200 pounds and then moderately, or (4) moderately for 200 pounds and then rapidly (18). Calves fed to gain moderately were no more efficient than were full-fed calves because of a longer total feeding period for those fed moderately which increased their total maintenance costs.

A similar trial was conducted by MacDonald (26) with three pairs of identical twin steers. One twin of each pair was on low energy intake while the other twin of each pair was placed on a higher level of intake. The low-intake group ingested two-thirds as much as the high intake

group but made only one-half the liveweight gains due to a higher proportion of feed used for maintenance in the low intake group. Gross efficiency, therefore, was much higher in the high-intake group.

Anderson (2) found that the digestibility of fresh green forages by wethers and of hays by steers was not affected by the level of intake. The digestibility of mixed diets decreased markedly as the level of consumption increased in two trials with steers. However, in three other trials the digestibility by steers of one of the same and two other mixed diets was not affected by the level of intake.

It should be pointed out here that the difference in intake that have been discussed with reference to efficiency and gains were not differences due to the inherent desires of the individual animal. The differences in intake were due to restrictions imposed upon a group or groups of animals while other groups were fed a more liberal ration. Since neither of the groups were full-fed ad libitum, it is unlikely that any inherent individual differences in consumption were expressed. It is probable that when all animals are allowed to consume food according to their individual desires the correlations of intake with efficiency and gain will be different from those noted when different nutritional levels are arbitrarily

imposed upon groups of animals.

The gross energetic efficiency of growth is influenced by the physiologic age of the animal under consideration because the older the animal the greater the maintenance tax in comparison to the productive increment (7, p. 58). Body size as such, when other conditions and - especially physiologic age - are equal apparently does not affect energetic efficiency. This phenomenon is not limited to within-species size differences but exists between species as well. The production per unit body weight is greater in small than in large animals, but the basal metabolism, or maintenance cost per unit body weight is also greater in small than in large animals with the net result that the two balance and the energetic efficiency is approximately independent of body weight (7, p. 53). In determining the caloric cost per pound of body weight produced in beef cattle MacDonald (27) found that while such cost varies markedly, the point of diminishing returns ranges from 850 to 1,100 pounds liveweight. In most of the categories it is reached in the liveweight range of 900 to 950 pounds.

Nelms and Bogart (33) have found that the age of the beef calf influences its efficiency of gain. For calves on a 300-pound test period, that is, from 500 to 800 pounds bodyweight, each increase of 10 days in age on test

brought about a corresponding increase of 4.2 pounds in TDN consumed per 100 pounds gain when corrections were made for maintenance. Although bull calves decreased in efficiency above maintenance more rapidly than heifers from body weights of 500 to 800 pounds, they nevertheless continued to be more efficient than heifers at 800 pounds liveweight. Ampy et al. working with the same herd but in a different year found that total feed required per unit of gain increased more noticeably in females than in males for the 500-to-800-pound test period.

A high correlation is generally found to exist between rate of gain and gross feed efficiency since, as mentioned earlier, the maintenance costs for any given weight gain are less for the faster growing individuals. A very high correlation between daily feed intake and daily gain has also been found to exist in swine. Wilham, Hazel and Durham (38) found a correlation of .90 between daily feed intake and daily gain within breed and season. The correlation between daily feed intake and efficiency of feed utilization was, however, insignificant. The correlation between daily gain and efficiency expressed as feed per unit of gain was -.6 for the total test period. In view of the generally high correlation between rate of gain and efficiency of gain and since the daily feed intake influences rate of gain, one might reasonably expect to

find a significant correlation between daily feed intake and feed efficiency.

Most of the investigations concerning feed consumption have dealt with differences brought about by (1) different feedstuffs, (2) varying energy levels of the rations, or (3) manipulation of various circulating metabolites and the destruction of hypothalamic structures. Although there are indications in the literature that inherent differences in feed consumption do exist, little or no attempt has been made to correct for environmental effects, sex, and weight variations so that genetically determined individual differences in feed intake may be ascertained.

MATERIALS AND METHODS

Biological Methods

The experimental material used in this study consisted of 290 beef calves which were born at Oregon State University during the years 1953 to 1958 inclusive. The calves were purebred Hereford and Aberdeen-Angus bulls and heifers. The Hereford herd consisted of three genetically distinct lines while the Angus calves were all of one line of breeding. Each of the four lines contained approximately 20 breeding females each year. It has been a general practice to use two bulls in each line for each year thus keeping inbreeding at a somewhat lower level than might otherwise be expected in lines of this size. The inbreeding coefficients ranged from zero to 35 per cent in 1958, the last year in which data for this study were taken. The average for the entire herd from which these data were taken was 8.42 per cent.

All calves used in this study were born in the spring during a period of approximately two months from March 1 to May 1. The calves and their dams were run on irrigated pastures and the calves were creep-fed in the years in which poor pasture conditions prevailed. The calves were weaned at approximately 425 pounds liveweight or on November 1 of each year. As the calves were weaned they

were placed under experimental conditions so that adjustments to the post-weaning environment were made before the feed-test period commenced at 500 pounds bodyweight. The feed test period was on a weight-constant basis and extended over the period from 500 to 800 pounds body weight.

All the calves used in the present study were fed a ration composed of one part concentrate mixture and two parts good quality half-ground, green, leafy alfalfa hay, thoroughly mixed and pelleted in a one inch pellet about one to one and one-half inches long. The ration was made up of the feed-stuffs indicated in Table 1.

A digestibility trial has been carried out on this feed by Nelms, Williams and Bogart (32). They report a somewhat increased feed intake due to pelleting. The pelleted ration also allows for a higher degree of accuracy in determining relative energy intakes. When a ration is not pelleted, calves may show a differential preference for some of the ingredients. With a pelleted ration, the feed refusal is the same proportionally as the ration originally offered the calf. Differences between calves in energy intake are thus dependent upon amount of feed eaten rather than upon individual preferences for the various ingredients in the ration. Hence, comparisons of total feed intake are, in effect, comparisons of total

Table 1. Analysis of O.S.C. Ration for Performance Testing Beef Cattle (166, p. 1)
Values Based on Morrison's Standards (163, Appendix I)*

Feedstuff	% of Ration	Dry Matter	T.D.N.	Net Energy (Therms)	Dig. Pro- tein	Crude Pro- tein	Ether Ex- tract	Crude Fibre	Ash	N.F.E.
Alfalfa										
No.2 grade	66.5	90.5	52.7	42.2	11.7	15.8	2.2	27.4	8.5	36.6
Molasses	5.0	80.5	60.8	68.1	4.4	8.4	-	-	8.8	62.0
Rolled Barley	15.0	89.8	78.7	71.4	6.9	8.7	1.9	3.7	2.6	70.9
Ground Oats	5.38	91.2	72.2	80.1	7.0	9.0	3.4	11.0	3.7	62.1
Beet Pulp	3.25	91.9	72.1	70.5	7.1	10.7	0.7	16.0	5.1	59.4
Wheat Bran	2.25	90.5	67.7	57.1	13.0	16.1	4.3	8.7	5.7	53.7
Soybean Meal (44%)	1.75	91.3	78.9	78.4	38.1	45.4	5.3	5.4	5.9	29.3
Linseed Meal (32%)	0.35	90.9	77.4	78.5	33.1	38.0	5.9	7.7	5.6	33.7
Steamed Bone Meal	0.175	96.3	-	-	-	7.1	3.3	0.8	81.3	3.8
Skim Milk	0.20	94.4	80.7	88.8	32.2	34.7	1.2	0.2	7.8	50.3
Yeast	0.009	93.9	70.2	-	41.9	48.7	1.1	5.5	6.4	32.2
Salt	0.15	-	-	-	-	-	-	-	-	-
Average Total Ration			59.5	52.2	10.8	14.3	2.28	20.5	7.26	45.33

* From MacDonald, M. A. Ph.D. Thesis

energy intake. The only manner in which a calf can increase its energy intake is to increase the amount of feed eaten.

The use of a pelleted ration also insures that any difference in circulating metabolites between calves is one of quantity or is due to an inherent difference in feed utilization. If, as has been suggested (24), appetite is influenced by circulating metabolites, then the use of a pelleted feed or some facsimile of such a ration would be quite important.

There is a relatively narrow temperature range during the months the calves are on test. The average annual temperature for the geographical area in which this study was conducted is 52.4°F. The range is from an average of 66.2°F in July and August to 39.3°F in January. The work of Johnson, Ragsdale and Yeck (21) indicates that temperatures as high as 80°F bring about a lowered feed intake in Shorthorn cattle. They found breed differences at 80°F that did not exist at 50°F. Brody (7, p. 305) gives a "comfort zone" of 60° to 70°F for farm animals. He indicates that farm animals, especially of the non-sweating class, are very much less sensitive to declining than to rising temperatures. He concludes that "the productivities, efficiencies and comfort of farm animals are not reduced by a decline in the environmental

temperature from the comfort zone to perhaps 0°F, while raising the temperature above 80° overheats and seriously reduces the productivities of non-sweating farm animals." In the present study the first calves went on test during October of each year and essentially all calves had reached 800 pounds liveweight and thereby completed the test by the first of the following August. On the basis of the work cited above as to the effect of environmental temperature upon feed consumption and rate of gain, it is probably safe to conclude that there is little or no effect of seasonal change upon food consumption in the present study.

The calves were penned in monosexual groups of six. Wood shavings were used for bedding, thus insuring that the pens contained no edible material other than the food regularly fed the animals. The calves were individually fed twice daily and were tied by neck chains for a period of three and one-half to four hours during each daily feeding period. Each calf was offered more food than it would eat so that ad libitum feeding was simulated. Individual automatic drinking cups were used, thereby providing fresh water to each calf at any time it was desired. The excess feed was removed from each feed bunk before the calves were turned loose each day and the weighback from each calf was weighed each week so that an accurate measurement of weekly feed consumption could be obtained.

The calves themselves were also weighed weekly at a uniform time and the weight change for each week was recorded along with the intake data.

Statistical Methods

The animals were fed over a weight-constant feeding period which extended from 500 to 800 pounds liveweight. In order to determine the patterns of intake, gain, and efficiency as the calves increased in age and weight, this three-hundred pound period was broken into four sub-periods. Each of these sub-periods were 75 pounds in length and the limits were as follows: (1) 500-575, (2) 576-650, (3) 651-725, and (4) 726-800. Since the weight of the animal influences each of the three traits, daily gain, daily consumption, and efficiency, it was felt that weight constant periods would be considerably superior to age-constant ones.

It is obviously impossible to correct for age in each period or for the total period in a weight-to-weight scheme of testing. Such corrections for age would theoretically make all animals the same weight at the same age, which is, of course, not the case at all. Some estimate of the effect of age can be had, however, by running regressions of the three dependent variables on age at 500 pounds. The regression obtained is not necessarily the

effect of age per se but rather may be the combined effects of all the factors which influence a calf's growth to 500 pounds. Such regressions for age at 500 pounds were determined and are presented in Table 8.

The effects of sex, line, year, and inbreeding of calf were estimated by the method of least squares (34). The model used was:

$$Y_{ijklm} = \mu + S_i + L_j + Y_k + F_l + e_{ijklm}, \text{ where:}$$

Y_{ijklm} = an individual measurement of either daily gain, daily feed consumption or feed efficiency expressed as pounds of feed consumed per pound of gain.

μ = an effect common to all animals.

S_i = the added effect of the i th sex, i = male or female.

L_j = the added effect of the j th line, j =
(1) Lionheart, (2) Prince, (3) David,
(4) Angus.

Y_k = the added effect of the k th year, k = 1953..
....1958.

F_l = the added effect of the l th degree of inbreeding, l = (1) 0%, (2) 1-10%, (3) 11-20%, (4) 21+%.

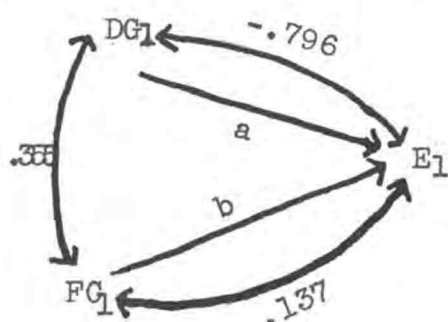
e_{ijklm} = random error, normally independently distributed with mean equal to zero and variance equal to σ^2 .

Intra-class correlations of each dependent variable with each of the remaining dependent variables have been calculated for the total period and for the sub-periods. The correlation of each dependent variable with itself in succeeding periods was also obtained. It should be

explained here that feed efficiency was expressed as pounds of feed consumed per pound of gain so that the negative correlations between gain and efficiency actually indicate that as gain increases efficiency also increases.

Path coefficients can be used in the statistical analyses of cause and effect in a system of correlated variables (23, p. 144). The coefficients themselves are not indicative of the casual relationship between variables; one must have a prior knowledge of which variables are the cause of variations in others. Given this knowledge we can obtain the coefficient of determination of two correlated variables on a third correlated variable such as exists in this study for the effect of feed consumption and rate of gain on efficiency.

The standard partial regressions needed for the path coefficients were calculated from the intra-class correlations (Table 7). For example:



$$\begin{aligned} r_{DG_1 E_1} &= a + b r_{DG_1 FC_1} \\ r_{FC_1 E_1} &= a r_{DG_1 FC_1} + b \end{aligned}$$

or

$$\begin{aligned} -.796 &= a + .355b \\ .137 &= .355a + b \end{aligned}$$

$$\begin{aligned} b &= .480 \\ a &= .966 \end{aligned}$$

$$\begin{aligned} R^2_{DG_1 FC_1 E_1} &= a^2 + b^2 + 2ab r_{DG_1 FC_1} \\ &= .933 + .230 - .329 \\ &= .824 \end{aligned}$$

The above method has been employed for the calculation of path coefficients in this study.

The heritability of daily feed intake was determined by regression of offspring on mid-parent as described by Falconer (15, p. 165-185). Due to the fact that intake data were available only for those animals calved from 1953 to 1958, the entire population could not be used in the calculation of heritability. Intake data were available for 66 mid-parent-offspring pairs so these animals were used to determine heritability of average daily intake over the 300 pound feeding period. Heritabilities were calculated using data adjusted for age at 500 pounds body weight and also using unadjusted data.

Half-sib analyses for the determination of heritability would have allowed the use of the entire population in the calculation of heritability. This method was not employed, however, due to a high degree of confounding of sires with lines and of sires with years. The intra-sire regression of offspring on dam (8) for determining heritabilities was not applicable in this case since a very limited number of dams per sire were available.

EXPERIMENTAL RESULTS

The effects of years, lines, sex, and inbreeding on rate of gain, feed efficiency, and daily feed consumption were determined by least squares analysis and are presented in Tables 3 and 3a. The significance of these effects were determined by analysis of variance and are presented in Table 2, while the raw means are given in Tables 4, 5, and 6.

Year Effects

Year effects for rate of gain were significant only in sub-period three. There was a significant difference for both feed consumption and for feed efficiency due to year in each sub-period and for the total period. During the years in which feed consumption was smallest, efficiency was highest so that rate of gain was remarkably constant over all years. There is no apparent time trend toward a greater or lesser efficiency or feed consumption.

Sex Effects

The effects of sex were significant at the .01 level of probability for all periods with respect to rate of gain and feed efficiency. However, the difference between the two sexes in daily feed consumption was quite small. The least squares estimates (Table 3a) indicate that at equal

Table 2. Analyses of Variance for Daily Gain, Feed Efficiency, and Daily Consumption by Sub-periods and for the Total Period

Source	D.F.	M.S.	M.S.	M.S.	M.S.	M.S.
Daily Gain						
Period		<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>Total</u>
Years	5	.6188	.1989	.8329**	.2169	.2194
Sex	1	20.7755**	22.2564**	34.7872**	24.8457**	24.4576**
Line	3	1.1953*	.7635*	1.7948**	1.6027**	.9764**
FC	3	.1775	.7149*	.1111	.0774	.0781
Error	277	.3333	.2685	.3253	.2546	.1990
Efficiency						
Period		<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>Total</u>
Years	5	11.2836**	11.3928**	18.9549**	36.1298**	13.6872**
Sex	1	204.0836**	274.6991**	534.1979**	479.4568**	323.3795**
Line	3	11.5254**	24.0370**	44.5422**	30.2642**	21.7689**
FC	3	3.9731	4.1924	3.3543	3.6307	2.9637
Error	277	2.4087	2.5142	4.5910	5.7464	1.6220
Daily Feed Intake						
Period		<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>Total</u>
Years	5	28.7580**	48.5204**	44.5731**	56.7840**	41.8278**
Sex	1	10.5881	5.9077	8.1786	15.4017	4.5676
Line	3	20.9548**	41.7126**	13.1382	21.2288*	20.2711**
FC	3	5.5888	3.5092	8.5046	4.8585	2.6088
Error	277	3.0054	2.5256	10.8138	7.3756	2.2426

* Significant at .05 level

** Significant at .01 level

weights females eat slightly more feed per day over the entire feeding period than do males. The males did eat somewhat more during the last period but the differences are not statistically significant for any period. The data in Table 3 show that the bulls were gaining more rapidly in any given period and therefore were more efficient than the heifers. The differences between the sexes in efficiency and daily gain were greater in periods 3 and 4 than in the first two periods (Tables 4 and 5).

Line Effects

The difference between lines in rate of gain was significant for all periods, but was more marked in the last two periods than in the first two. The calves in the Angus line gained least rapidly in all periods, but they were almost equal to the calves in the David line in period one. Overall, the three Hereford lines were quite similar in daily gain with the calves in the Lionheart line being very slightly inferior to those in the Prince and David lines. All three of the Hereford lines became increasingly superior to the Angus line as weight increased from 500 to 800 pounds (Tables 3 and 4).

Line differences were evident for feed efficiency during each of the four sub-periods and over the total feeding period as shown in Table 2. The Prince line was the most efficient line in all periods. The animals in

Table 3. Least Squares Estimates of Factors Affecting Daily Gain and Feed Efficiency

<u>Daily Gain</u>					
<u>Period</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>Total</u>
<u>M</u>	2.423624	2.330163	2.215272	2.297098	2.293836
Year 53	.112296	-.055407	.094712	.045382	.038250
Year 54	.197939	.128026	.316776	.083929	.167037
Year 55	.165740	.067364	.173070	-.081520	.063143
Year 56	.158866	-.004365	.346069	.099518	.154338
Year 57	.363060	.068801	.171598	.061701	.129387
Females	-.553489	-.574850	-.716214	-.605283	-.600537
Lionheart	.304340	.171914	.269808	.344493	.233327
Prince	.149713	.256136	.395709	.330815	.266175
David	.308799	.214297	.310721	.302439	.273634
Inbreeding 1-10	.017976	.173520	.100853	.065574	.090921
Inbreeding 11-20	-.059187	.281560	.096460	.002969	.054355
Inbreeding 21+	.059954	.122405	.139241	.024830	.080522
<u>Efficiency</u>					
<u>Period</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>Total</u>
<u>M</u>	7.292647	8.486261	9.426165	10.782704	8.800113
Year 53	-1.061184	-.588757	-1.137987	-2.076276	-.983419
Year 54	-.802623	-.602628	-1.585362	-1.558919	-.862751
Year 55	-.389574	.333261	-.175336	.138469	.291056
Year 56	-.273815	.138754	-1.106531	-1.339601	-.366630
Year 57	-1.326935	-.923837	-1.121431	-1.049787	-.963026
Females	1.734751	2.012620	2.806624	2.658936	2.183682
Lionheart	-.881351	-.731252	-1.577123	-1.191861	-1.034642
Prince	-.909435	-1.470579	-1.912507	-1.620498	-1.365849
David	-.849870	-.736327	-1.205514	-1.141433	-.875552
Inbreeding 1-10	.006939	-.439205	.077018	-.518456	-.396667
Inbreeding 11-20	.429346	-.551546	.323277	-.271111	-.208092
Inbreeding 21+	-.039064	-.135830	-.233789	-.655672	-.635520

* Year 1958 = Sex male = Line Angus = Inbreeding 0.
 Year, sex, line and inbreeding are deviated from these quantities.

Table 3a. Least Squares Estimates of Factors Affecting Feed Consumption and Age at 500 Pounds

Period	Daily Feed Intake				Total
	1	2	3	4	
<u>M</u>	16.146004	18.556641	19.411972	21.806779	18.882677
Year 53	-1.236408	-1.584950	-1.858286	-2.811585	-1.778463
Year 54	-.417994	-.561206	-.622297	-1.350585	-.665651
Year 55	.749885	1.211525	1.090688	.389457	1.034600
Year 56	.760227	.344384	.312631	-.797481	.239853
Year 57	-.717184	-1.222651	-.606992	-1.290141	-.749302
Females	.395131	.295149	.347275	-.476561	.259525
Lionheart	.071180	-.302071	-.116302	.733659	.009320
Prince	-1.173417	-1.459109	-.657700	-.663742	-1.022842
David	.168475	.054471	.425180	.227040	.144113
Inbreeding 1-10	.534648	.538545	.503174	.622294	.447971
Inbreeding 11-20	.796444	.641127	.928739	.218256	.594222
Inbreeding 21+	.367173	.758882	.327058	.174932	.523506

Period	Age of Calf			
	1	2	3	4
<u>M</u>	222.620630	253.416860	287.577500	323.719470
Year 53	-.259482	.258082	1.028799	-.952386
Year 54	-3.435440	-2.960948	-4.667354	-6.053098
Year 55	-4.967138	-6.058650	-7.568253	-8.031109
Year 56	.079758	.198688	-.750887	-4.278119
Year 57	-.324095	-2.900531	-4.932480	-5.948714
Females	.265895	.335471	.412051	.513784
Lionheart	1.584155	.054691	-2.850587	-8.821684
Prince	11.828610	11.293141	7.602995	1.037464
David	17.336304	14.204564	11.686846	4.947998
Inbreeding 1-10	-.313653	-2.508557	-4.503446	-7.720618
Inbreeding 11-20	18.129935	16.982028	14.971832	13.438128
Inbreeding 21+	10.853719	10.985193	6.142411	5.673510


* Year 1958 = Sex male = Line Angus = Inbreeding 0.

Year, sex, line and inbreeding are deviated from these quantities.

the Lionheart line were not markedly inferior in any given period and overall were almost equal to the Prince calves in feed efficiency. The David Herefords were third in efficiency with the Angus being considerably inferior to all the Hereford lines. A comparison of the Angus line with the Herefords reveals a pattern similar to that found for rate of gain, that is the superiority of the Hereford lines over the Angus becomes greater as the animals proceed from 500 to 800 pounds body weight (Table 3). The data in Table 5 indicate that calves in all lines become less efficient as they increase in weight and that this trend is most marked in calves of the Angus line.

The differences between lines in feed consumption were statistically significant for all periods except sub-period 3. The Lionheart, Angus, and David calves were not greatly different in daily intake but the Prince calves ate considerably less feed per day than did calves of the other three lines. The difference in lines in feed consumption tends to become smaller as body weight approaches 800 pounds (Table 3a). The Lionheart calves consumed somewhat less food per day than the Angus which in turn ate slightly less than the David calves. The relatively small daily feed intake of calves in the Prince line is primarily responsible for the superiority of this line in efficiency since the rate of gain of calves in the three

Table 4. Raw Means by Subclasses for Daily Gain in Each Sub-period and for the Total Period

	No.	DG ₁	DG ₂	DG ₃	DG ₄	TDG
	290	2.47	2.41	2.36	2.28	2.33
Female	143	2.17	2.08	1.96	1.94	2.02
Male	147	2.76	2.73	2.75	2.61	2.65
Lionheart	59	2.58	2.47	2.40	2.42	2.44
Prince	77	2.50	2.59	2.59	2.44	2.47
David	61	2.69	2.56	2.55	2.42	2.50
Angus	93	2.23	2.13	2.02	1.96	2.05
Fx 0	44	2.23	1.99	1.96	1.94	2.00
Fx 1-10	97	2.46	2.39	2.35	2.30	2.33
Fx 11-20	109	2.49	2.58	2.45	2.34	2.39
Fx 725	41	2.62	2.43	2.48	2.37	2.43

DG = Daily gain

Table 5. Raw Means by Subclasses for Feed Efficiency in Each Sub-period and for the Total Period

	No.	E ₁	E ₂	E ₃	E ₄	TE
μ	290	7.11	8.14	9.03	9.90	8.38
Female	143	8.04	9.27	10.57	11.36	9.59
Male	147	6.20	7.03	7.53	8.48	7.20
Lionheart	59	6.94	8.08	8.60	9.68	8.12
Prince	77	6.61	7.07	7.97	8.85	7.51
David	61	6.63	7.85	8.52	9.22	7.90
Angus	93	7.93	9.24	10.51	11.35	9.58
Fx 0	44	7.45	9.25	9.87	11.08	9.42
Fx 1-10	97	7.00	8.00	8.99	9.73	8.29
Fx 11-20	109	7.13	7.70	8.85	9.65	8.16
Fx 725	41	6.74	8.24	8.46	9.44	7.86

E = Feed efficiency

Table 6. Raw Means by Subclasses for Daily Consumption in Each Sub-period and for the Total Period

	No.	FC ₁	FC ₂	FC ₃	FC ₄	TFC
<i>M</i>	290	16.52	18.57	19.83	21.03	18.97
Female	143	16.69	18.70	19.93	20.72	19.06
Male	147	16.34	18.43	19.72	21.32	18.87
Lionheart	59	16.89	18.85	19.89	21.98	19.30
Prince	77	15.54	17.43	19.20	20.24	18.08
David	61	16.90	19.07	20.32	21.09	19.33
Angus	93	16.82	19.00	19.98	21.02	19.25
Fx 0	44	15.98	18.19	19.06	20.22	18.44
Fx 1-10	97	16.38	18.41	19.59	21.15	18.81
Fx 11-20	109	16.70	18.53	20.15	20.96	19.04
Fx 725	41	16.53	18.98	19.85	21.27	19.25

FC = Daily feed consumption

Hereford lines is very similar.

Effect of Inbreeding

The level of inbreeding had only a small effect upon rate of gain. The differences in daily gain due to level of inbreeding were statistically significant ($P=.05$) only in period three but the mean difference in daily gain consistently favored the inbreds over the non-inbreds. There was also a consistent, although non-significant, trend toward greater feed consumption by inbred animals (Table 3a).

The intra-class correlations of the three dependent variables, daily gain, daily intake, and feed efficiency are presented by periods in Table 7. The correlations between periods for each dependent variable are given also.

The correlations between daily gain and feed efficiency are high, as would be expected, since efficiency in this case is gross efficiency. The correlations between daily gain and efficiency are negative due to the fact that feed efficiency is expressed as pounds of feed per pound of gain. A high negative correlation thus means that the calves that gain more rapidly require less feed per pound of gain.

The correlations between daily gain and feed consumption are moderate and are very similar for all periods

Table 7. Intra-Class Correlations by Periods Involving Daily Gain, Efficiency and Feed Consumption

	DG2	DG3	DG4	TDG
DG1	.129	.197	.148	.395
DG2	-	.033	.085	.312
DG3	-	-	.019	.364
DG4				.361
	E2	E3	E4	TE
E1	.065	.210	.226	.416
E2		.007	.194	.283
E3			-.044	.382
E4				.380
	FC2	FC3	FC4	TFC
FC1	.468	.215	.131	.919
FC2		.378	.149	.702
FC3		-	.096	.695
FC4				.453
	E1	FC1		FC1
DG1	-.796	.355	E1	.137
	E2	FC2		FC2
DG2	-.780	.363	E2	.025
	E3	FC3		FC3
DG3	-.654	.345	E3	.205
	E4	FC4		FC4
DG4	-.716	.156	E4	.113
	TE	TFC		TFC
TDG	-.700	.345	TE	.269

DG = Daily gain

E = Feed efficiency

FC = Daily feed consumption

1, 2, 3, 4, % refer to periods

except the last one. These correlations are positive and indicate that the animals that eat the most gain the most or vice-versa as the case may be.

The correlation of feed consumption with efficiency was rather small in all periods. All correlations between these variables were positive, revealing that in this study increased daily consumption is associated with a small decrease in efficiency.

The intra-class regressions of the three dependent variables on age at 500 pounds (Table 8) show that calves that are older at the beginning of the test period gain slightly more, have a higher daily intake and are somewhat less efficient than are the younger calves. These effects are not necessarily due to age but may be a summation of all the factors that influence gain during the suckling period. It can be seen from Table 3a that females are older than males at any given weight. The calves in the Angus line have the lowest average age during the first two periods, but the Lionheart calves reach 800 pounds at a younger average age than do calves of any of the other lines. The Prince and Angus calves reach 800 pounds at virtually the same age while the David calves were somewhat slower in attaining the final weight.

The group with 1-10 per cent inbreeding was younger at any given weight than were the non-inbred calves. The

two groups that were inbred more than 10 per cent (11-20 and over 20 per cent) were older at any given weight than were the non-inbreds. The age gap between the non-inbreds and those inbred in excess of 10 per cent narrowed, however, as the animals progressed from the first to the fourth period.

The coefficients of determination for two of the independent variables on the third have been calculated by the method of path coefficients and are presented in Table 9. It appears that rate of gain and efficiency have relatively little effect upon daily feed consumption. However, daily gain and feed consumption influences efficiency very markedly as one might expect. Also, feed consumption and efficiency had a marked effect on rate of gain.

A heritability of .38 has been found for daily feed consumption (Table 10) when the data were adjusted for age at 500 pounds. This adjustment was made since the suckling environment may exert some influence upon the daily feed intake during the post-weaning period. The heritability estimate was slightly lower (.28) when feed consumption was not corrected for differences in age at 500 pounds body weight.

Table 8. Intra-Class Regressions of Traits on Age at 500 Pounds

	<u>Initial Age</u>		<u>Initial Age</u>		<u>Initial Age</u>
DG1	.0075	E1	.0266	FC1	.0573
DG2	.0069	E2	.0309	FC2	.0623
DG3	.0060	E3	.0360	FC3	.0648
DG4	.0059	E4	.0400	FC4	.0662
TDG	.0064	TE	.0326	TFC	.0629

DG = daily gain

E = efficiency

FC = feed consumption

1, 2, 3, 4 and T refer to periods

Table 9. Path Coefficients Involving Daily Gain, Feed Consumption and Efficiency by Periods

		Period				Total
		1	2	3	4	
*R ²	Daily gain and feed consumption on efficiency	.834	.718	.710	.578	.786
*R ²	Daily gain and efficiency on feed consumption	.606	.374	.443	.051	.125
*R ²	Feed consumption and efficiency on daily gain	.853	.771	.667	.569	.824

* Coefficient of determination

Table 10. Heritability of Daily Feed Intake Estimated by Regression of Offspring on Mid-Parent

	Mid-parent offspring pairs	b ± s.e.	Heritability
Adjusted for age at 500 pounds	66	.384±.15	.38
Unadjusted for age at 500 pounds	66	.283±.15	.28

DISCUSSION

Years

There is a remarkable lack of variation between years with respect to rate of gain, especially since efficiency differed considerably from year to year. There was, however, a very consistent relationship between feed efficiency and daily consumption so that during the years in which consumption was relatively high, efficiency was relatively low. This observation suggests strongly that daily intake increases at the expense of efficiency. It is possible that the energy content of the feed may have varied between years and that eating habits were influenced by such energy levels. As stated earlier, however, every effort was made to insure a minimum amount of variation in the feed from year to year. In view of the precautions taken it seems unlikely that the energy content of the feedstuff varied enough from year to year to account for the between-year differences in feed consumption and in feed efficiency. It seems more likely that year differences in the pre-test environment were present and that the adequacy of the environment for the calves during the suckling period influenced their feed consumption and consequently their feed efficiency. It could very well be that the preweaning environment has a greater influence

upon intake and efficiency than upon growth rate during the postweaning feed test period. This concept will be brought out later under the section on compensation of this discussion.

Relationship Between the Dependent Variables

The correlations between the dependent variables indicate that the association of rate of gain with efficiency is quite high and that daily gain and daily consumption are associated to a lesser extent. There is a small inverse relationship between efficiency and intake, that is, in general the more the calves eat the less efficient they are. A high correlation between gain and gross efficiency is usually found since the animals that gain fastest require less time per unit gain and therefore less of the feed consumed is utilized for maintenance in rapidly growing animals (5, p. 290) (18, 26). This is particularly true when the feeding period is on a weight-to-weight basis as is the case in the present study.

The inverse relationship between daily intake and efficiency is not particularly surprising since similar results have been obtained by other workers (7, p. 90-91). If feed is restricted for one group of animals and their efficiency is compared to that of a more liberally fed group, then efficiency is usually greatest in the high

intake group due to the fact that a higher percentage of the feed consumed is used for maintenance in the animals on restricted intake (18, 26) (7, p. 90). When calves are fed ad libitum, however, increased intake apparently brings about a lower feed utilization and lessens the net energy obtained per unit of feed consumed. The slight increase in daily gain associated with such increased consumption apparently is not great enough to offset the decreased utilization of feed; thus a lower gross efficiency is observed. If intake is influenced by rate of passage of feeds as is suggested by Blaxter et al. (3) and Crampton (8) then increased consumption may bring about a less complete breakdown of ingested nutrients. This would be particularly true with high roughage rations where the cellulose and hemicellulose must be broken down in the rumen in order to be utilized by the animal.

The positive correlation between daily gain and feed intake was as expected and is in line with Brody's assumption that the greater the feed consumption the more rapid is the growth of the animal (7, p. 90). The magnitude of the correlation is only moderate, however, thus indicating that the level of consumption is not solely responsible for the variations in rate of gain even when the animals are on the same feed and adjustments have been made for sex, line, year and inbreeding.

Although the correlations are expressions of the relationship between two variables, they indicate nothing as to the cause and effect relationships. The path coefficients (Table 9) tend to confirm the theory that calves gain more because they eat more and not vice-versa. There is little doubt that rate of gain affects gross efficiency. It seems quite probable, however, that efficiency also has a large effect upon rate of gain since efficiency and daily consumption account for the greatest portion of the variation observed in rate of gain in this study. The inherent ability of the animal to efficiently utilize absorbed nutrients is probably the most important factor in determining rate of gain.

Correlation Between Periods

The data in Table 7 show that the correlation of rate of gain in one period with rate of gain in succeeding periods was much lower than would be expected. Two factors are primarily responsible for these low correlations between periods. First of all, the calves in the different lines did not maintain the same relative positions throughout the test period with respect to rate of gain. The Prince calves were the poorest of the Hereford lines in gain during the first period, but were the best line in rate of gain in periods two and three. The Lionheart

calves were at the top in periods one and four but were slightly inferior to the other two Hereford lines in the second and third period.

The data for this study were set up so that the final weight in one period was the beginning weight of the next period. An error such as overweighing or excessive amount of fill at the end of a weight period would act to increase rate of gain in that period, but would act to lower rate of gain in the following period. This is probably partially responsible for the low correlations between sub-periods while the correlation between each period and the total period was somewhat larger.

The between-period correlations for efficiency and consumption show the same pattern as those for rate of gain, and can be explained on the same basis as that given above for rate of gain.

Sex

As was pointed out previously, there was no significant difference between sexes with respect to feed consumption. The males gain much more rapidly than do the females but this more rapid gain is due to a higher efficiency of feed conversion and not to a higher energy intake per unit of body weight.

It is not clear just what effect the more rapid gains of the bulls have on their feed consumption. It is

possible that intake may be influenced to some extent by the rapidity of gain. The effect of age upon daily intake must be considered here also, since older calves consume somewhat more feed daily at a given weight than do younger ones (Table 8). Since the males are gaining faster, but the females are older at any given weight, it is quite possible that the effect of increased gain in the bulls is counterbalancing the effect of age in the heifers, thus the daily consumption of the two sexes is the same. These data are not such that one can predict the relative feed consumption of the two sexes if both were of an equal age and gaining at the same rate.

Inbreeding

The inbred calves in this study were not significantly different from non-inbred animals in daily intake and feed efficiency. There was a statistically significant difference due to inbreeding in period two for rate of gain, however, over the total period, rate of gain was quite similar for inbred and non-inbred calves. The least squares estimates for age in Table 3a show that the group of inbreds with 1-10 per cent inbreeding were as young at 500 pounds body weight as were the non-inbreds. This means, of course, that the suckling gain of this group of calves was equal to that of non-inbred calves. This is

verified by a study that was made on these same animals during their suckling period (unpublished data). This group became younger at a given weight as the feed test period progressed from 500 to 800 pounds since the calves in this inbred group had a slightly more rapid gain than did the non-inbreds.

The inbred group with 11-20 per cent inbreeding and those that were above 20 per cent in inbreeding were older at the beginning of the test period as is shown in Table 3a. They too gained slightly faster than did the non-inbred calves, ate a little more feed per day and were a little more efficient. The group that was inbred 1-10 per cent exhibited an overall superiority over both the remaining inbreds and the non-inbred calves as is shown by their greater weight per day of age. This superiority is probably a genetic one since they were not inferior in suckling gain and were somewhat superior in postweaning gain.

Heritability

It is not known at the present time whether the calculated heritability of .384 for daily feed consumption is representative for the entire beef cattle population since there apparently has been no heritability estimates calculated in other herds for this trait. It is possible that in other herds under different management schemes the

heritability estimates of daily feed consumption would vary markedly.

The type of ration fed would probably have quite a large effect upon the calculated heritability of feed intake. For instance, on a high concentrate ration the relative capacity and rate of passage of food through the digestive tract would probably have less influence upon feed intake than they would if an all-roughage diet were fed. In the case of high concentrate feeding all calves may be able to eat enough to satisfy completely their inherent energy demands. Differences between calves in daily intake on a ration of this sort would therefore be a reflection of the inherent energy demands of the various calves. On the other hand, if the ration is made up entirely of roughage, none of the calves may be completely satisfying their energy requirements so that full growth potential can be realized; consequently the capacity of the digestive tract and the rate of passage of foods are the important factors influencing feed intake. The heritability of daily intake on a high concentrate diet would thus be determined by inherent energy requirements while the heritability of daily intake on a high-roughage diet would be determined by the inherent capacity of the digestive tract and by the rate of passage of foods through

the alimentary canal.

Further work is needed in this area before it can be determined whether the heritability of daily feed intake is generally high, moderate, or low. The use of a laboratory animal, such as the guinea pig, should be profitable in determining heritability of daily intake on different kinds of rations.

Compensation

There is evidence in this study that compensation for environmental limitations in the suckling period is occurring during the post-weaning feed test period.

In a previous study conducted at this station (14) involving this same experimental herd it was found that the lines ranked as follows in order of most rapid suckling gain to least rapid: (1) Angus, (2) Lionheart, (3) Prince, and (4) David. The rankings from most rapid to least rapid gain during the postweaning period were exactly reversed, that is, (1) David, (2) Prince, (3) Lionheart, and (4) Angus (Table 3). The relatively less rapid gain of the Angus calves in the postweaning period is probably not due entirely to their own compensatory reactions or to compensation by the Hereford lines, but rather to the fact that the Angus cattle have a smaller mature size and mature somewhat earlier than do the

Herefords. They may thus possess less potential for growth in the test period, particularly as they approach 800 pounds than do the Hereford calves. This Angus herd is definitely superior, however, to the Herefords of this study in milk production. No information is available on feed consumption and efficiency for the suckling period so the relative position of the calves in the four lines during the pre- and post-weaning periods cannot be established for these two factors.

Additional evidence for compensation in this study is furnished by the intra-class regression of rate of gain upon age at 500 pounds (Table 8). The regressions show that the calves that are oldest at 500 pounds bodyweight eat more, gain slightly more, and are less efficient during the succeeding test period than calves that reach 500 pounds at an earlier age. An increase in age at 500 pounds is indicative, of course, of a relatively low suckling rate of gain, therefore, the calves that are gaining more slowly in the preweaning are gaining most rapidly during the postweaning period. If this phenomenon is not due to compensatory mechanisms then one must assume that different sets of genes are involved in determining gain in body weight during the suckling and feed test period. Furthermore, it would require that selection for an increase in one would bring about a decrease in the other.

This is, perhaps, a possibility but it seems a rather unlikely one.

In work involving identical twin steers Winchester found that calves that were placed on a restricted feed intake during one period showed compensation during succeeding periods (40, p. 17). de Baca (10, p. 85) also found that animals which in one period endure a restriction in growth due to environmental influences tend to compensate for these restrictions in the next period. The results of the present study are in good agreement with these conclusions reached by the two workers cited above. This study does not, however, agree with Winchester's findings on efficiency of compensatory gain. He has reported that even though the restricted animals reached slaughter weight from 10 to 20 weeks later than did their cotwins, the former attained this weight on approximately the same intake of energy as did the latter (40, p. 33). The regression of efficiency on age at 500 pounds given in Table 8 in the present study indicates that the compensatory gain is somewhat more costly due to the higher daily consumption of the older calves. The compensation that occurred in the calves making up this study was apparently due primarily to increased consumption rather than to increased efficiency.

The difference in the efficiency found for compensatory gain in this study and that found by Winchester (40) is very interesting. In his study the restricted co-twins were on feed from 10 to 20 weeks longer than were the calves on a liberal ration and yet the gross efficiency for total gain was approximately the same. It is certain that the total maintenance requirements of the calves on the restricted diet were considerably greater than that for those on a liberal ration, therefore the efficiency of gain above maintenance must have been tremendous. Winchester's data show that almost without exception the retarded twin consumed more energy per day after being placed upon a liberal ration than did the twin that had been liberally fed all along (40, p. 11-16). For the entire trial the rate of gain per day was higher for the liberally fed than for the restricted animals but the usual high association between rate of gain and efficiency seems to have been lacking (39, p. 10). The animals in Winchester's study exhibited compensation for both rate and efficiency of gain while those in the present study showed compensation for rate of gain only. Apparently if the increased gain due to increased age at a given weight, that is compensatory gain, is great enough the gross efficiency of such gain may be very high.

The restriction imposed upon the steers in Winchester's study was one of energy alone. Furthermore, when liberal feeding was resumed the ration offered was high in concentrates and thus energy required to fulfill maximum growth potential could be obtained.

Unlike the conditions in Winchester's experiment the restrictions during the suckling period in this study were deficiencies of the entire diet. Also unlike Winchester's study the liberal ration in this study was a high roughage one and the animals probably could not consume enough additional feed to markedly increase their energy supply. The lowered efficiency associated with increased consumption in this study may be due to a more rapid rate of food passage in the high intake calves, which in turn results in a less complete utilization of feed.

In the present study it appears that any increase in gross efficiency one might expect as a result of the greater feed test gains made by calves that were inferior during the suckling period had been more than offset by the effect of increased feed consumption.

Inbreeding and Compensation

The data (unpublished) collected on these animals during the suckling period also allows the calves to be ranked by inbreeding groups for rate of gain. Again,

ranking from most rapid to least rapid gain the following order was found: (1) 1-10 per cent, (2) 0 per cent, (3) + 20 per cent, (4) 11-20 per cent. The ranking for the postweaning period is: (1) 1-10 per cent, (2) above 20 per cent, (3) 11-20 per cent, and (4) 0 per cent. The evidence for compensation is not so clear-cut here since the relative positions of all groups are not reversed completely from one period to the next as was the case when they were ranked by lines.

It is possible to break this population into only two groups according to inbreeding, namely inbred calves and non-inbred calves. When this is done and the relative positions of the two groups are compared for pre- and post-weaning gain, it is found that the non-inbred calves are superior in suckling gain, but that the inbred group is very slightly superior in the postweaning period. If this is to be regarded as compensation, it requires that the calf compensate for its own inbreeding which is, of course, a genetic rather than an environmental factor. Such compensation is not impossible and may even occur in this herd but there is an alternative explanation that seems more likely in the present study. It is generally conceded that inbred animals are less well buffered to environmental change than are non-inbred ones. Thus, the

inbred calves may have a genetic potential for growth equal to, or even superior to that of non-inbred calves if both were under an ideal environment. Under a poor environment, however, the inbred calves would probably gain less rapidly than the non-inbred ones. If the environment were changed for the better the inbred calves would be expected to more nearly approach their genetic potential and could gain as rapidly as the non-inbred animals even though no compensation was involved. There is little doubt that the post-weaning environment under which the calves in the present study are handled is superior to their suckling environment. This is particularly true of the Hereford calves since their dams are much poorer in milk production than are the Angus cows.

Implication with Respect to Selection Criteria

The least squares estimates for age (Table 3a) show that the Lionheart calves are younger at the conclusion of the test period than are any of the other lines. As stated earlier this line ranks second in suckling gain (14) and is a close third in rate of gain on test. This observation points up the importance of weight per day of age or some facsimile as a criterion for selection, since even though the Lionheart calves were not the top line in either period, they were overall the best line in the herd.

Weight per day of age as a basis for selection is most effective, of course when more than one growth period has elapsed before selection takes place. For instance, if selection is carried out at the end of the suckling period there would be no particular advantage of using weight per day of age over daily gain. Selection on the basis of suckling gain alone is not desirable due to the fact that suckling gain is, to a large extent, an expression of the milking ability of the dam rather than the genetic potential of the calf for growth. This fact is pointed out in this study by the younger age of the calves in the Angus line at 500 pounds (Table 3a) and the subsequent decline in their age advantage throughout the test period. Selection based on postweaning gain alone is also undesirable since restrictions in the suckling period bring about compensatory growth. Therefore, selections based on rate of gain on feed test would inevitably result in selection for lowered milk production. This would be most undesirable since the gains during the suckling period are far cheaper than are gains during the postweaning period.

Feed efficiency is an extremely important trait and is generally given a place in the selection index whenever sufficient records are kept so that this quantity can be calculated (5, p. 188). Gross feed efficiency is so

highly correlated with rate of gain (Table 7) that selection for one automatically brings about some selection for the other. An increase in the age of the calf at a given weight acts to lower this correlation, however, since the older calf gains slightly more but his feed efficiency is less than that of a younger calf at the same weight (Table 8). This again points out the importance of a high suckling gain since the age of the calf at any given weight on test is greatly influenced by its suckling gain.

It does not appear desirable at the present time to include appetite in the selection criteria used for a breeding program. In the first place, daily intake is considerably more difficult to determine than is daily gain and secondly, its relationship to rate of gain and efficiency is not of sufficient magnitude to warrant giving it a great deal of attention in a selection program.

There is a distinct possibility that the relationships between appetite and daily gain and between appetite and gross efficiency would be of a greater order of magnitude if the ration fed were composed entirely of roughage. It seems logical to expect that this would be the case since the higher the concentrate level in a ration, the less feed the animal needs to ingest to satisfy its energy requirements. The difference between individuals in feed consumption would be expected to increase as the proportion

of roughage-to-concentrate increased and thus there would be a corresponding boost in the effect of daily consumption upon daily gain.

There is little question that heritable individual variations in appetite do occur. Contrary to Blaxter's (3) observation that little or no individual variations in appetite occur among animals of equal size, it is apparent in the present study that all animals of the same body weight do not eat the same amount of food. That this difference is inherent is indicated by the line differences and by the heritability figure of .384 calculated for daily feed consumption on a weight-constant basis.

As the beef industry moves in the future toward leaner carcasses, lighter marketing weights and more roughage feeding it is quite likely that the appetite of the animal or its capacity for roughage will be a much more important factor in production than it is at the present time.

SUMMARY AND CONCLUSIONS

A study was conducted on 290 beef calves from four lines of breeding to determine the influence of years, sex, line and inbreeding upon rate of gain, feed efficiency and daily feed consumption during a 300-pound post-weaning feed test period. Intra-class correlations were obtained and path coefficients were calculated in order to determine the relationship between rate of gain, feed efficiency and daily feed intake. Regressions upon age at 500 pounds were run to estimate the influence of the suckling environment upon each of these traits.

The results of these analyses support the following conclusions:

1. Even though daily feed consumption and feed efficiency have varied over the years involved in this study, rate of gain has remained remarkably constant.
2. At equal weights there is no appreciable difference between males and females with respect to daily feed intake. They do vary markedly in rate of gain and efficiency with males being superior to females in both traits.
3. There are significant differences for lines in rate of gain, efficiency and daily feed consumption.

The calves in the Angus line deviate considerably from those in the three Hereford lines in these traits and are inferior to the Herefords in all three characteristics.

4. There are no significant effects of inbreeding upon any of the three variables mentioned above. There is, however, a consistent trend for the inbred calves to eat more, gain more and be slightly more efficient than are the non-inbred calves.
5. The intra-class correlation between rate of gain and efficiency is high; that between rate of gain and daily consumption is moderate, while the correlation between daily consumption and efficiency is quite low.
6. The correlations indicate that a high rate of gain is associated with a high feed efficiency and a relatively high feed consumption. The association between daily feed intake and efficiency is such that calves that eat more are somewhat less efficient.
7. The regressions of rate of gain, feed efficiency and daily intake upon age at 500 pounds indicate that as age at the beginning of the test period

increases the calves gain slightly faster, eat more and are less efficient.

8. There is evidence in this study that unfavorable conditions in the suckling period induce compensation in the post weaning period. Such compensation for adverse pre-weaning conditions appears to be due primarily to increased feed intake rather than to increased efficiency.
9. This study indicates that weight per day of age is the most reliable criterion for selection when more than one growth period is involved.
10. It is apparent in this study that all animals at a given weight do not eat the same amount of food. That the differences in daily intake are heritable is indicated by line differences and by a heritability figure of .384 calculated for daily consumption. This estimate of heritability was obtained by the regression of offspring on mid-parent.
11. It is concluded that under feeding conditions existing at the present time in which high concentrate rations are fed beef cattle, selection for appetite would probably not be desirable from an economic standpoint.

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