THE RELATIONSHIP BETWEEN BODY WEIGHT, DAILY GAIN AND EFFICIENCY OF FEED UTILIZATION IN BEEF CATTLE

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INTRODUCTION

One fundamental purpose of beef cattle breeding is the production of cattle capable of making high quality beef with the most economical use of feed. As early as 1835, Amos Cruickshank in his selection of breeding stock, paid particular attention to the middles of his cattle with the idea that animals having large digestive capacity were efficient utilizers of feed. Somewhat this same concept is followed by cattlemen of today in their breeding and feeding programs regarding efficiency of feed utilization. Characteristics of body conformation such as body capacity and strong heart girth are considered as indicators of efficiency. These characteristics may indicate efficiency, but since they are subjective measurements and hard to evaluate with precision, the breeder may have difficulty in measuring relative merit among his animals. The job would be simplified if there was some objective measure of efficiency. For a measure of efficiency to be readily applicable to field conditions, it should be easy to apply and require no special techniques.

The ratio of feed to gain or feed required per pound of gain is the common measure of efficiency. Winters and McMahon (1933) and Knapp and Baker (1944) reported low correlations between rate of gain and efficiency when weight was ignored. This implies that selection on the basis of observed efficiency would discriminate against fast gaining animals unless all animals under consideration were of equal weight.

To study this problem adequately, more information is needed on the relationship between feed consumption and weight as well as daily gain and weight. Studies of other factors which influence feed consumption and efficiency are also needed. The general objective of this study was to investigate certain factors that may influence feed intake and have a bearing on the measurement of efficiency in beef cattle.

REVIEW OF LITERATURE

Lambert et.al. (1936), in reviewing the role of nutrition in genetics research, raised the problem of finding a suitable measure for efficiency. They explained that efficiency was too complex in character to be measured by the gross efficiency of gain per unit weight of feed consumed. While this was the most important single factor, it was by no means the only one which deserved consideration. They proposed that methods developed by Titus, Jull, and Hendricks (1934) be used to study the relation between live weight and cumulative feed consumption.

Titus, Jull, and Hendricks, (1934), applied the curve of diminishing increment, as described by Spillman and Lang, (1924), to the relationship between feed consumption and growth in chickens. The curve of diminishing increment, $W = A - BR^F$, described with a high degree of accuracy, the relationship between feed consumption and live weight over a wide range of levels of feed intake.

Morris, Palmer and Kennedy, (1933), in a study of feed requirements for the growth of the rat, found that at the end of six generations of selecting two lines of rats for high and low levels of efficiency of feed utilization,[1] the low efficiency line was

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[1] Defined as $\frac{\text{digestible dry matter consumed}}{\text{gain in live weight}} \div$ mean weight during the experiment x 100.

forty percent less efficient and was more variable than the high efficiency line. This would definitely suggest that heritable factors influence the efficiency of feed utilization.

Winters and McMahan, (1933), studied efficiency variations in 62 steers. They reported that steers of essentially the same weight, breeding, age, market grade and condition, exhibited differences in their abilities to make economical gains. At least a four month feeding period was needed to determine the relative efficiency[1] of an animal. Feed consumed on the basis of average body weight was not a satisfactory indication of an animal's efficiency in feed utilization. The correlation between rate and efficiency of gain was 0.34. However, when these data were corrected for mean live weight differences, the correlation became 0.71. In their opinion, average daily gain was the most useful, practical measure of daily gain.

Knapp and Baker, (1944), studied the correlation between rate and efficiency of gain in steers. The correlation between rate and efficiency of gain was 0.49. After adjusting the steers to a constant weight, the correlation was 0.89, indicating that daily gain could be used to predict efficiency with a high degree of accuracy when comparing animals of the same size. However, com-

[1]Defined as $\frac{\text{Pounds of gain}}{\text{T.D.N. x 100}} \times \frac{\text{Mean live weight}}{100}$

parisons of gross efficiency made between animals not the same size would be misleading and often erroneous.

Knapp, et.al., (1941), in studying progeny testing in Hereford cattle, found that daily gain and efficiency of gain were not highly correlated, and that ultimate efficiency of gain, or rate of gain, could not be predicted with appreciable accuracy from previous rate of gain during the suckling period or from conformation score at weaning time. They reported a correlation of 0.44 between daily gain and efficiency of gain.

Black and Knapp, (1936), reported a correlation of 0.88 between average daily gain and economy of gain.

Kunkel, Colby, and Lyman, (1953), reported a high correlation between efficiency of gain and serum protein bound iodine level. However, this high correlation exists only within a certain range. Apparently, the optimum level is between 4.0 and 4.9 μg per 100 ml. serum. Animals with serum protein bound iodine above or below this level showed lower rates of gain and efficiency of gain.

Knapp and Nordskog, (1946), estimated the heritability of efficiency of gain by intra-class correlation and sire:progeny regression. Their estimates were 75 percent by intra-class correlation, and 48 percent by sire:progeny regression. They pointed out that these estimates were higher than seemed reasonable and the causes of these high estimates were not known.

In summary, it may be said that investigations have reported that heritable factors influence efficiency of food utilization. There is general agreement that a high correlation exists between daily gain and efficiency of utilization when comparing animals of the same size.

SOURCE OF DATA

The data used for this study were collected on bulls and their steer progeny in Beef Cattle Record of Performance feeding tests conducted at Blacksburg and at Front Royal, Virginia, over a period from 1947 to 1952.[1]

Bulls of Shorthorn, Hereford, and Angus breeds were represented. However, all three breeds were not represented each year. The steer progenies were the offspring of bulls, selected for high and low rates of daily gain, and grade Hereford cows. The bulls and steers were on full feed for each test period, and all animals were fed individually. Twice a day, hand feeding was practiced from 1947 to 1949 and self feeding from 1950 to 1952. Individual weights and feed records of both the bulls and steers by 14 and 28 day intervals were available. The data consisted of periodic weights and feed consumption of each animal. The numbers of animals, number of days on feed, and observations per animal by years and groups are shown in Tables 1 and 2.

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[1]This is a cooperative project with the Virginia Agricultural Experiment Station, United States Department of Agriculture and State Experiment Stations of the Southern Region cooperating.

Table 1. Number of Animals per Group, Total Number of Days on Feed, Number of Periods and Length of Each Period by Years.

Year	Groups			Total Number Days on Feed	Number of Periods	Length of each Period
	Hereford[1]	Angus[1]	Shorthorn[1]			
1947-48	8			162	6	14 and 28
1948-49	20			134	6	14 and 28
1949-50 S_1	6	11		112	8	14
1949-50 S_2	7	5		154	11	14
1950-51	10	8	5	168	6	28
1951-52	12	15	14	168	6	28

[1]Number of Head

Table 2. The Number of Sire Groups, Total Number of Steers, Total Number of Days on Feed, Number of Periods, and Length of Each Period by Years.

Year	No. of Sire Groups	Total No. of Steers	Total No. of Days on Feed	Number of Periods	Length of each Period
1950-51	8	30	196	7	28
1951-52	10	36	204	11	varies

METHODS OF INVESTIGATION

The investigation was conducted in two phases. The objective of the first phase was to evaluate the relationship between body weight and daily feed consumption, and to investigate the importance of some other influencing factors in daily feed intake. The objective of the second phase was to find a suitable, practical measure of efficiency.

Relationship Between Weight and Feed Consumption

It has been suggested that the curve of diminishing increment, described by Spillman and Lang (1924), expresses the relationship between feed consumption from birth to maturity with a high degree of accuracy. According to data reported by Guilbert and Gregory (1952), the growth curve of cattle from birth to maturity has a segment that extends from six to eighteen months which is approximately linear. For the purposes of this investigation, it was thought that the linear regression would describe the relation between weight and daily feed consumption with sufficient accuracy.

The data on feed consumption were studied by analyses of variance and covariance (Snedecor, 1946), to determine the amount of variation contributed by various sources, and to evaluate the relation between weight and daily feed consumption.

The analyses were made within years because comparisons between years were complicated by having a completely different set of animals fed each year which made it impossible to separate yearly environmental differences from animal differences. Looking at the situation purely from the genetic point of view, selections are usually made among contemporary animals.

The sums of squares for the analysis of daily feed intake were adjusted by the linear regression of daily feed consumption on body weight. A straight line regression of feed consumption on weight describes the linear relationship between feed consumption and weight, but does not consider the possibility that some non-linear function may be a more accurate description of the true relationship.

The analyses of variance and covariance were as follows:

Source of Variation	Degrees of Freedom
Periods	(k-1)
Groups	(m-1)
Groups x Periods	(m-1)(k-1)
Animals-within-groups	(n-m-1)
Regression	1
Residual (Animals-within-groups x Periods Adjusted for Regression)	(n-m-1)(k-1)-1

Where:

k = number of periods
m = number of groups
n = total number of animals

The animals-within-groups and period (error) regression was used in making the adjustments for weight differences. The adjusted variances measure the deviation of each of the observations for periods, groups, etc., from the within-group and period regression line. The error regression line should be the best estimate of the true relation between weight and daily feed intake, since it estimates the tendency of animals within a group to eat feed in proportion to their body weight during a given period.

The mean squares were interpreted as follows:

Source of Variation	Interpretation of Mean Squares
Periods	$nP + \bar{n}BP + R$
Groups	$\bar{n}kB + kA + \bar{n}BP + R$
Groups x Periods	$\bar{n}BP + R$
Animals-within-groups	$kA + R$
Regression	$(n-m-1)(k-1)\,L + R$
Residual (Animals-within-groups x Periods Adjusted for Regression)	R

Where:

$\bar{n}$ = average number of animals per group[1]
k = number of periods
m = number of groups
n = total number of animals

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[1]Since the groups have varying numbers, the exact $\bar{n}$ is obtained from the following equation: $\bar{n} = \frac{1}{m-1}\left(\sum_{i=1}^{m} h_i - \sum_{i=1}^{m} h_i^2 \Big/ \sum_{i=1}^{m} h_i\right)$

Where: h = number of animals in a group and m and n are the same as before. However, when the variation in group numbers is small, the coefficient found by the solution of the previous equation is approximately the same as the average number of animals in each group. The average number was used throughout this study.

and

P = period contributions to variance
BP = group period interaction contributions to variance
B = group contributions to variance
L = linear effects
R = residual error contributions to variance

Since the coefficients, $\bar{n}$, k, m, and n could be determined from the number of animals, groups and periods within each year, estimates of P, B, A, L, and R were obtained by equating the mean square interpretations to the observed mean square values and solving the resulting equations simultaneously.

It is pointed out that the interpretation of the regression mean square is not based on rigorous mathematical proof, and this investigator has been unable to find any interpretation of it in the literature. The above interpretation is based on intuitive reasoning. It is hoped that this paper will introduce the problem of its interpretation and perhaps lead to a more rigorous mathematical solution.

Relationship Between Daily Gain and Efficiency

Several investigators have studied the relationship between average daily gain and efficiency of feed utilization (see Review of Literature) and found varying degrees of correlation. Efficiency as defined in this study was:

$$E = \frac{D}{F}(100)$$

Where:

E = efficiency
D = average daily gain for the entire feeding period
F = average daily feed consumption for the entire feeding period

The relationships between D, E, and F were investigated by correlation and partial regression methods (Snedecor, 1946) with D, as observed, and F and E, both as observed and as adjusted for weight differences. The relationship between daily gain and time was studied by analyses of variance as follows:

Source of Variation	DF
Groups	m-1
Periods	k-1
First two periods vs. remaining periods	1
Linear trend in first two periods	1
Linear trend in remaining periods	1
Quadratic trend in remaining periods	1
Residual variation in remaining periods	k-5
Error	(m-1)(k-1)

Any trends indicated by this analysis could be inferred to exist with weight since weight would be increasing with time. The first two periods were separated from the remaining periods because daily gains appeared small when the animals were going on feed and through an adjustment period. Average daily gain after the animals were on feed was thought to be a better estimate of the true gaining ability of each animal.

The investigation of the unadjusted data did not reveal any consistent relationship between D, E, and F. However, when the data were adjusted for weight differences, the correlation between E and D were consistently high.

The regression equation $E(F) = \bar{F} + b(W-\bar{w})$ was used to adjust for weight differences

Where:

$E(F)$ = expected feed consumption when weight was equal to the average weight of the group
F = observed average daily feed consumption for each animal
b = within group regression coefficient
W = average weight of an animal during its feeding trial
$\bar{w}$ = average weight of the group

The adjusted efficiency was $\frac{D}{E(F)}(100)$.

The partial regression coefficients which show the amount and direction of influence of D and E on F, were calculated both for the adjusted and unadjusted data. They were calculated by the following equations:

$$B_{EF.D} = \frac{r_{EF} - r_{FD}\, r_{ED}}{1 - r^2_{FD}}$$

and

$$B_{ED.F} = \frac{r_{ED} - r_{EF}\, r_{FD}}{1 - r^2_{FD}}$$

Where:

$B_{EF.D}$ = the regression of E on F with D held constant

$B_{ED.F}$ = the regression of E on D with F held constant

and

r_{ED} = the correlation between E and D

r_{FD} = the correlation between F and D

r_{EF} = the correlation between E and F

Heritability of Feed Consumption

Heritability was defined as:

$$H = \frac{G}{G + C + P + BP + R}$$

Where:

H = heritability of average daily feed consumption
G = component of variance due to additive genetic differences among animals fed in the same year
C = component of variance due to environmental differences among animals in the same sire group
P = component of variance due to differences among periods in the feeding trial
BP = component of variance arising from group-period interactions
R = variance component due to random environmental variations of the same animal from period to period

The data on the steers, which were groups of half sibs, were used in obtaining estimates of heritability. No genetic interpretation could be placed on the bull data.

Estimates of P, BP, and R were obtained directly from Table 9. These components were adjusted for weight differences and were considered to be true estimates of the real effects contributed by each source.

Estimates of G and C were obtained from the group (B) and animal (A) components. B and A were interpreted as follows:

(1) $B = 1/4\ G$ or $4\ B = G$

(2) $A = 3/4\ G + C$

Since B and A were obtained from the analyses of variance, estimates of G and C were obtained by solving equations 1 and 2.

RESULTS

Relationship Between Weight and Daily Feed Consumption

The means of the weights and daily feed consumption are shown by periods, groups and years in Tables 3 and 4.

The weights and daily feed for the bulls and steers were condensed to 28 and 56 day averages respectively, for the sake of clarity and ease of presentation. For this reason, the degrees of freedom in the analyses of variance do not agree with the number of periods shown in the tables.

It is evident from Tables 3 and 4 that factors other than weight are affecting daily feed intake. For example, in the 1949-1950 bulls, both groups ate approximately the same amount of feed per day and yet there was a difference of 80 pounds in average body weight. In other instances, (1951-1952 bulls), the variability in feed consumption from period to period was high and after the first half of the test, the group intermediate in weight ate the most feed. The daily feed consumption of the steers fed in 1951-1952 showed a definite quadratic trend. The data on hand do not show any cause for this trend except that the last period for this particular group of animals extended to May 4th and climatic conditions might have influenced feed consumption.

Table 3. Average Daily Feed Consumption and Weights of Bulls by Years, Breeds and 28 Day Periods.

Period		I		II		III		IV		V		VI		Average	Average Feed per
Year	Group	Weight	Feed	Weight	Feed	Weight	Feed	Weight	Feed	Weight	Feed	Weight	Feed	Weight	Day
1947-48	Hereford	538	15.20	594	17.40	669	18.40	720	21.90	769	24.61			658	19.50
1948-49	Hereford	560	11.90	616	13.40	660	15.48	715	16.38	770	16.48			644	14.73
S_1	Angus	724	16.85	758	23.72	808	22.31	855	24.65					786	21.88
1949-50	Hereford	875	19.15	905	26.08	967	25.12	1037	25.83					946	24.04
	Average	800	18.00	832	24.90	888	23.72	946	25.24						
S_2	Angus	426	8.50	464	12.36	492	15.92	552	16.70	610	19.32	662	21.04	534	15.64
1949-50	Hereford	521	8.46	546	11.76	569	17.14	624	16.74	686	21.16	740	23.90	614	16.53
	Average	474	8.48	505	12.06	530	16.53	558	16.72	648	20.24	701	22.27		
1950-51	Angus	456	11.30	510	16.61	581	16.25	632	18.06	708	17.35	746	18.99	606	16.44
	Shorthorn	486	12.30	532	16.68	610	17.40	664	19.18	752	19.38	782	21.86	641	17.80
	Hereford	431	10.35	471	13.34	530	13.39	579	14.82	643	15.12	691	17.10	558	14.02
	Average	464	11.32	504	15.54	574	13.71	625	17.35	701	17.28	740	19.32		
1951-52	Angus	564	14.67	629	18.19	677	18.74	740	19.90	797	20.89	844	21.75	648	16.91
	Shorthorn	517	13.21	577	17.51	635	18.73	694	20.12	769	22.27	832	23.63	670	19.25
	Hereford	514	13.20	566	16.15	615	16.59	672	17.09	728	18.53	795	19.88	708	19.02
	Average	532	13.69	591	17.28	642	18.02	703	19.04	765	20.56	824	21.75		

Table 4. Average Daily Feed Consumption and Weights of Steers by Years, Sire Progenies and 56 Day Periods.

Year	Periods / Group	I Weight	I Feed	II Weight	II Feed	III Weight	III Feed	IV[1] Weight	IV[1] Feed	Average Weight	Average Feed
1950-51	1	415	14.98	512	18.43	642	22.55	758	25.70	557	17.20
	2	425	17.04	524	19.38	649	22.35	742	24.18	562	20.25
	3	482	16.92	566	20.98	711	25.19	840	27.22	623	21.91
	4	476	17.03	572	20.58	706	23.30	808	26.08	617	21.13
	5	458	17.44	546	19.35	653	20.78	752	24.52	581	19.95
	6	518	17.09	624	21.45	750	25.28	860	28.27	580	22.30
	7	408	17.24	486	19.12	618	24.55	740	26.48	538	20.75
	8	408	16.05	517	19.35	612	21.18	707	25.33	540	19.79
	Avg.	449	16.72	543	19.83	668	23.15	776	25.97		
1951-52	A	436	13.92	516	16.92	652	21.38	784	18.31	587	17.63
	B	503	16.70	584	19.02	728	21.56	836	19.15	662	19.11
	C	380	11.78	436	14.02	568	20.63	674	16.50	515	15.73
	D	426	13.71	508	15.74	645	21.11	768	16.42	587	16.75
	E	482	15.84	582	20.46	694	25.07	824	22.70	646	21.02
	F	516	16.44	608	21.86	750	24.54	870	19.82	686	20.66
	G	505	16.60	602	21.44	754	24.36	858	16.36	680	19.69
	H	468	16.23	553	21.70	700	24.74	802	20.46	630	20.78
	I	406	13.87	436	17.44	622	22.10	727	17.45	560	17.71
	J	435	15.12	532	20.18	668	25.08	782	20.16	604	20.13
	Avg.	456	15.02	536	18.88	678	23.06	793	18.73		

[1] Period IV is 28 days long in the 1950-51 group and 56 days long in the 1951-52 group.

The analyses of variance of feed consumption are shown in Table 5. These data show that differences among the following sources of variation were significant or highly significant: periods in all years; groups in all years except S_1 and S_2 of 1949-1950 bulls; group-period interactions in all years except the S_2 of 1949-1950 bulls and 1951-1952 steers; and animals-within-groups in all years except 1947-1948. In short, all the sources of variation other than random errors showed significant influences on daily feed consumption in most of the years.

Table 6 shows the analyses of variance of daily feed consumption adjusted for regression on weight. These data show that after adjustment for weight, the differences among the following sources of variation were significant or highly significant: periods in all years; groups in 1950-1951, 1951-1952 bulls, and 1950-1951 steers; group-period interactions in all years except 1951-1952 steers; animals-within-groups in all years except 1947-1948; and regression in all years except S_1 of 1949-1950 bulls.

The components of variance and the percentages of the total variance contributed by each component are shown before and after adjustment for regression in Tables 7, 8, 9, and 10. These components indicate that periods and animals-within-groups were the major contributors, other than random error, to the total variance.

Table 5. Analysis of Variance of Daily Feed Consumption Before Adjustment For Regression.

Source of Variation[1]	BULLS												STEERS			
					S1		S2									
	1947-48		1948-49		1949-50		1949-50		1950-51		1951-52		1950-51		1951-52	
	DF	MS	DF	MS	DF	MS	DF	MS	DF	MS	DF	MS	DF	MS	DF	MS
Periods	4	112.02**	5	74.55**	7	226.13**	10	272.87**	5	155.61**	5	331.66**	6	401.33**	10	474.88**
Groups	-	-----	-	-----	1	23.18	1	4.15	2	164.23**	2	71.94**	7	24.22**	9	132.02**
Groups x Periods	-	-----	-	-----	7	8.91*	10	5.86	10	2.60	10	10.21**	42	13.64**	90	8.01
Animals-within-group	7	0.59	19	12.67**	15	43.73**	10	14.05**	20	21.62**	38	27.60**	22	17.36**	26	42.84**
Error	28	0.27	95	0.45	105	3.79	100	3.90	100	1.40	190	1.85	132	2.15	260	7.78

[1]Significance was tested by using the interpretation of the mean square to test the significance of each component.

* Significant at $P \leq 0.05$
**Significant at $P \leq 0.01$

Table 6. Analysis of Variance of Daily Feed Consumption Adjusted for Regression on Weight.

Source of Variation[1]	BULLS												STEERS			
					S_1		S_2									
	1947-48		1948-49		1949-50		1949-50		1950-51		1951-52		1950-51		1951-52	
	DF	MS	DF	MS	DF	MS	DF	MS	DF	MS	DF	MS	DF	MS	DF	MS
Periods	4	9.45**	5	7.55**	7	65.20**	10	36.24*	5	27.81**	5	29.60**	6	9.53*	10	341.13**
Groups	-	----	-	----	1	0.24	1	12.07	2	34.48**	2	57.59**	7	8.24	9	42.10**
Groups x Periods	-	----	-	----	7	8.22*	10	10.82**	10	3.65**	10	6.21**	42	3.17*	90	8.10
Animals-within-groups	7	0.62	19	2.21**	15	13.09**	10	10.90**	20	11.35**	38	9.60**	22	9.74**	26	19.74**
Error Regression	1	1.96*	1	0.45	1	9.87	1	49.15**	1	26.88**	1	122.71**	1	15.41**	1	34.33*
Residual Error	27	0.27	94	0.45	104	3.09	99	3.44	99	1.15	189	1.21	131	2.05	259	7.67

[1]Significance was tested by using the interpretation of the mean square to test the significance of each component.

* Significant at $P \leq 0.05$
** Significant at $P \leq 0.01$

Table 7. Theoretical Components of Variance Before Adjustment for Weight Differences.

	BULLS						STEERS	
	1947-48	1948-49	S_1 1949-50	S_2 1949-50	1950-51	1951-52	1950-51	1951-52
Periods	13.970	3.705	8.061	22.414	6.652	7.840	13.256	12.969
Groups	-----	-----	(- 0.378)	(-0.181)	3.061	0.438	0.203	2.398
Groups x Periods	-----	-----	0.602	0.327	0.016	0.610	0.392	0.064
Animals-within-groups	0.062	2.037	1.163	0.923	3.370	4.292	2.173	3.187
Error	0.270	0.450	3.790	3.900	1.400	1.850	2.150	7.780
Total	14.302	6.192	13.616	27.564	14.499	15.030	18.174	26.398

The negative components were ignored in obtaining the total variance and the percent of variance from each source.

Table 8. Percent of the Total Variance Contributed by Each Source Before Adjustment for Regression.

	BULLS						STEERS	
	1947-48	1948-49	S_1 1949-50	S_2 1949-50	1950-51	1951-52	1950-51	1951-52
Periods	0.977	0.598	0.592	0.813	0.459	0.522	0.729	0.491
Groups	-----	-----	0.000	0.000	0.211	0.029	0.011	0.091
Groups x Periods	-----	-----	0.044	0.012	0.001	0.041	0.022	0.002
Animals-within-groups	0.004	0.329	0.085	0.033	0.232	0.286	0.120	0.121
Error	0.019	0.073	0.278	0.141	0.097	0.123	0.118	0.295

Table 9. Theoretical Components of Variance After Adjustment for the Error Regression of Average Daily Feed Consumption on Weight.

	BULLS						STEERS	
			S_1	S_2				
	1947-48	1948-49	1949-50	1949-50	1950-51	1951-52	1950-51	1951-52
Periods	1.156	0.355	3.352	2.118	1.050	0.570	0.212	9.251
Groups	----	----	(-0.264)	(-0.094)	0.447	0.523	(-0.098)	0.554
Groups x Period	----	----	0.604	1.230	0.325	0.365	0.295	0.119
Animals-within-groups	0.084	0.293	1.250	0.678	1.700	1.398	1.099	1.097
Regression	0.063	0.000	0.065	0.457	0.257	0.639	0.101	0.102
Error	0.200	1.098	3.090	3.440	1.150	1.210	2.050	7.670
Total	1.503	1.746	8.361	7.923	4.929	4.705	3.757	18.793

The negative components were ignored in obtaining the total variance and the percent of variance from each source.

Table 10. Percent of the Total Variance Contributed by Each Source After Adjustment for Error Regression.

	BULLS						STEERS	
			S_1	S_2				
	1947-48	1948-49	1949-50	1949-50	1950-51	1951-52	1950-51	1951-52
Periods	0.769	0.203	0.401	0.267	0.213	0.121	0.056	0.492
Groups	----	----	0.000	0.000	0.091	0.111	0.000	0.029
Groups x Period	----	----	0.072	0.155	0.066	0.078	0.079	0.007
Animals-within-groups	0.056	0.168	0.150	0.086	0.345	0.297	0.293	0.058
Regression	0.042	0.000	0.008	0.058	0.052	0.136	0.027	0.006
Error	0.133	0.629	0.369	0.434	0.233	0.257	0.545	0.408

Group and group-period interaction contributions account for only a small fraction of the total variance in feed consumption. The group and animals-within-groups contributions were smaller in years when hand feeding was practiced (1947-1950) than when self feeding was practiced.

The degrees of freedom for group differences among the 1950-1951 and 1951-1952 steers may be divided into progeny of fast gaining sires versus progeny of slow gaining sires, and progeny within fast and slow gaining sires. Table 11 shows the subdivision.

Table 11. Subdivision of Group Variance into Progeny of Fast Gaining Sires vs. Progeny of Slow Gaining Sires and Within Fast and Slow Gaining Sires, Adjusted for Regression.

	1950-1951		1951-1952	
Source of Variation	DF	MS	DF	MS
Fast vs. Slow Gaining Sire Progenies	1	11.33	1	18.46
Progenies within Fast & Slow Gaining Sires	6	7.56	8	45.05**
Residual Error	131	2.05	259	7.67

The differences among progenies within fast and slow gaining sires were highly significant in 1951-1952. The data did not indicate any significant differences in the feed consumption of the progenies of fast and slow gaining sires provided they are of equal weight.

The Relationship Between Average Daily Gain and Efficiency of Feed Utilization

Efficiency of feed utilization is usually reported as some ratio of feed and gain. According to the previous analyses, differences in feed consumption were partially explained by weight difference. Therefore, it would seem that weight should be considered in making comparison of efficiency. The relationship between average daily gain, average daily feed consumption, and efficiency were examined before and after adjustment for weight differences.

The relationship between observed average daily gain, average daily feed consumption and efficiency of feed utilization for 1950-1951 and 1951-1952 bulls were analyzed by correlation and partial regression methods. The correlation and partial regression coefficients for the 1950-1951 and 1951-52 bulls were as follows:

	r_{ED}	r_{EF}	r_{FD}	$B_{EF.D}$	$B_{ED.F}$
1950-1951	-0.05	-0.54	0.88	-2.22	1.91
1951-1952	0.50	0.42	0.38	-0.71	0.76

These data do not indicate any consistent relationship between average daily gain or average daily feed intake and efficiency. The partial regression coefficients show a negative relationship between efficiency and average daily feed consumption and an approximately equal positive relationship between efficiency and daily gain.

The means and analyses of variance of average daily gains are shown in Tables 11 and 12 respectively. There were no significant group differences in daily gains in any years. The gains during the first two periods were significantly different from those in remaining periods in 1949-1950 S_2 bulls and 1951-1952 steers. Table 12 shows there was a marked tendency for daily gain to be low during the first two feeding periods. The residual variation in periods, after removal of the difference between the first two and the other periods, was significant in 1950-1951 bulls, and 1950-1951 and 1951-1952 steers. This residual variation was examined for trends by orthogonal polynomials. The only significant trend found was a quadratic trend in 1950-1951 bulls. It was concluded from this analysis that no consistent trend existed with time in these data except in the adjustment period when the animals were going on feed. Although this analysis examines the relation between daily gain and time, any trends or lack of trend, in average daily gain could be inferred to exist with weight since weight was increasing with time. For this reason, daily gain was not adjusted for weight differences in studying efficiency.

Table 12. Average Daily Gains (Pounds Per Day) by 28 Day Periods and Years.

Year	PERIODS 1	2	3	4	5	6	7	Average
1949-50 S_2 Bulls	1.12	0.91	2.05	2.14	1.90			1.62
1950-51 Bulls	1.67	2.48	1.83	2.71	1.38			2.01
1951-52 Bulls	2.11	1.84	2.13	2.24	2.11			2.09
1950-51 Steers	1.52	1.58	2.04	2.53	1.78	2.97		2.07
1951-52 Steers	1.07	1.00	2.77	2.18	2.68	1.95	1.57	1.89
Average	1.50	1.56	2.16	2.36	1.97	2.46	1.57	

Table 13. Analysis of Variance of Periodic Daily Gains.

Source of Variation	BULLS 1949-50 S_2 DF	MS	1950-51 DF	MS	1951-52 DF	MS	STEERS 1950-51 DF	MS	1951-52 DF	MS
Groups	1	0.0410	2	0.0964	2	0.1010	7	0.1043	9	0.1050
First 2 Periods vs. Remaining Periods	1	2.4766**	1	0.0344	1	0.1232	1	6.5052	1	20.2810*
Residual Variation in Periods[1]	3	0.0345	3	1.2500**	3	0.0446	4	1.6753**	5	2.0304**
Error[2]	4	0.0309	8	0.0952	8	0.0725	35	0.1699	54	0.2898

[1]The significance of Residual Variation in Periods was tested by Error.
[2]The significance of any trend in periods was tested by the Residual Variation in Periods.

* Significant at $P \leq 0.05$
** Significant at $P \leq 0.01$

The correlation and partial regression coefficients between daily gain and adjusted feed intake and efficiency are shown in the following table.

	r_{ED}	r_{EF}	r_{FD}	$B_{EF.D}$	$B_{ED.F}$
1950-1951	0.84	0.08	0.26	-0.15	0.88
1951-1952	0.77	0.39	0.17	0.27	0.73

The correlation between efficiency and average daily gain shows that daily gain can be used to measure efficiency of feed utilization with a high degree of accuracy. The partial regression coefficients also indicate that average daily gain was more important as an indicator of efficiency than daily feed consumption with weight held constant.

The observed data on the 1950-1951 and 1951-1952 steers for gain and efficiency showed correlations of 0.63 and 0.46 respectively, and the correlations between adjusted efficiency and daily gain were 0.88 and 0.83, indicating that daily gain alone can be used to measure efficiency with rather good precision.

Estimate of the Heritability of Feed Consumption

Estimates of the heritability of feed consumption were obtained on the steers. The component for group differences (B) among the 1950-1951 steers was -0.098, and indicates no genetic influence for that year. Theoretically, a negative variance component is explained as being due to sampling error or some bias in the data. The group component for 1951-1952 was 0.552. It was assumed that differences in these components were due to sampling and they were combined for an estimate of heritability.

Components obtained by pooling the means squares (Table 6) for the two years were:

Periods =	6.546
Groups =	0.342
Groups x Periods =	0.204
Animals-within-groups =	1.081
Residual Error =	5.786

The estimate of heritability from these values was as follows:

$$A = 1.081 = 3/4\,G + C$$
$$B = 0.342 = 1/4\,G$$
$$G = 1.368$$
$$C = 0.055$$

and

$$H = \frac{1.368}{6.546 + 0.204 + 5.786 + 0.055 + 1.368}$$

$$H = \frac{1.368}{13.959} = 0.098$$

DISCUSSION

The analyses of variance and covariance data in this study show that although weight has a significant influence on feed consumption, other factors such as periods, groups, group-period interactions and differences among animals in the same group also influence feed intake.

The components of variance before adjustment for weight differences showed that period was, by far, the largest contributor to the total variance. Adjusting for weight by regression reduced the period component to approximately the same size as random variability among animals. The size of the period component indicates that it is an important factor in certain types of feeding trials. In weight constant feeding tests, comparisons made between animals fed in different periods, even though they were the same weight, would contain differences due to periods. Since it is impossible to estimate, statistically, the variance due to periods unless the animals are fed in the same periods, precise analyses of such data can not be made. In time constant feeding tests with all animals fed over the same period, comparison of feed consumption during the test periods can contain considerable variation due to weight differences and may not reflect real differences in the efficiency of feed utilization. However, in time constant feeding trials, the variance due to differences among periods can be estimated and weight can be controlled statistically. Thus it seems that more reliable information can be obtained from time constant feeding trials than from weight constant feeding trials.

Group differences account for approximately 5% of the total variance after adjustment for weight. The differences among steer groups contain a genetic component, but the nature of genetic differences among breeds is so complex that no plausible genetic interpretation is possible. During the years in which hand feeding was practiced (1947-1950), differences among groups after adjusting for regression were not significant, and the variance components for group differences in these years were small negatives. On the other hand, in the years (1950-1951 and 1951-1952) when self feeding was practiced the group components were all positive and in some cases accounted for a significant fraction of the total variance. Since there were only two years with more than one group of animals, it is not possible to state definitely that hand feeding obscured group differences, but the data suggest that hand feeding can obscure the detection of group differences, even though the animals are supposedly fed to the limit of their capacity.

The group-period interactions are especially important. They were highly significant in several years, and the components of variance indicate they can be a relatively large source of variation. These interactions are probably due to an interaction between heredity and environment. There is no other apparent reason for periods affecting some groups differently from others. The group-period interactions indicate that several periods should be used in the comparison of efficiencies, since efficiency may vary from period to period. Feeding trials on winter feeding rations and in record of performance feeding tests would need to be long enough for these interactions to average out.

The component of variance for group-period interaction was occasionally increased by adjusting for weight differences. The reason can be seen by referring to Tables 3 and 4. In some periods, groups showing large differences in weight, showed only small differences in feed consumption. In such cases, when the group variance of feed was adjusted for weight, variance of feed consumption was increased.

The mean squares for animals-within-groups were significant in every year except one, and the component before and after adjustment for regression show it to be a major source of variation along with periods and residual error. This clearly indicates that individual feed records are important, and that variation in ability to utilize feed may be large even among animals of the same sire group. This is in agreement with the findings of Winters and McMahan (1933), who reported that steers of essentially the same breeding, weight, age, market grade and condition, varied in their abilities to utilize feed.

The animals-within-groups variance component was smaller when hand feeding was practiced than when the animals were self fed. The differences among animals-within-groups accounted for approximately 10 percent less of the variance when the animals were hand fed than when they were self fed. These data indicate that animals falling in the extreme upper or lower ends of the feed consumption distribution would probably not be detected. This would not be so important in testing winter feeding rations, but is of great importance in genetic studies in growth and efficiency of feed utilization, since the most desirable and undesirable animals, from the standpoint of efficiency, could not be identified.

The animals-within-groups variance component also shows that if the maximum information is to be obtained from feeding tests, each animal should be individually fed. Approximately 18 percent of the total variance is accounted for by differences among animals-within-groups while only 5 percent of the total variance is due to group differences. Thus, in group feeding trials about 12 percent of the information is lost. In statistical studies made on group feeding data, this 12 percent would be added to the error variance and decrease the precision of estimates of animal differences.

The regression of daily feed consumption on weight accounts for a significant amount of the variance in every year except one. Regression reduced the mean square by large amounts, especially those for periods and animals-within-groups. The components show that adjusting for feed consumption by regression on weight, reduced the total variance by approximately 35 percent which makes it evident that the precision of feeding experiments can be increased by controlling weight.

In winter feeding and pasture tests, it is usually possible to control weight by experimental design, but in record of performance tests when a random sample of a sire progeny or breed is being tested, one must use statistical methods. Weight can be controlled fairly easily by covariance methods. However, when the relationship departs from linearity, the procedures become more complicated. It is entirely possible that some non-linear function may express more accurately the relationship between weight and feed consumption than the linear function this author has assumed, even for the short segment of the growth curve examined in this study. Assuming that some non-linear function expresses the true relationship it appears questionable if the increased precision would justify the extra labor involved. This problem needs further investigation.

The analyses of covariance showed that feed consumption is partially determined by weight. This has important applications in studies of efficiency. Efficiency is usually reported as the ratio of gain to feed, feed per 100 lbs. gain or some similar method. According to the analyses of covariance, such figures will be misleading unless the animals being compared are of equal weight. If the animals are not of equal weight, variation in efficiency may not reflect the true animal differences, and may be due to variation in weight only. Even though large and small animals are making the same gains, the large animals will be penalized because of larger body maintenance requirements and thus the small animals will appear the most efficient. Ideally, efficiency should be compared on the basis of feed required per pound of gain above body maintenance. However, since it seems likely that animals of the same size may have different maintenance requirements, the next best alternative would be to adjust feed consumption to an average weight or to find some measure of efficiency other than the ratio of gain to feed.

The second phase of the study investigated the relationship between observed and adjusted efficiency and daily gain. The correlation between daily gain and observed gross efficiency ranging from -0.05 to 0.63 indicated the relationship between daily gain and observed gross efficiency is low and that selection on the basis of gross efficiency would be misleading and often erroneous. Table 14. gives examples of the kind of mistakes that would arise from selection on the basis of gross efficiency among animals of different weights.

Table 14. Liveweight, Gain, Feed Consumption and Efficiency without and with Correction for Weight of a Group of Hereford Bulls Fed in 1950-1951.

Average Weight	Daily Gain	Daily Feed		Efficiency	
		Observed	Adjusted	Observed	Adjusted
378	1.34	9.67	15.50	13.86	8.64
450	1.71	10.32	14.42	16.57	11.86
484	1.55	11.17	14.46	13.88	10.72
526	2.05	13.93	16.21	14.72	12.65
630	2.02	15.45	15.23	13.07	13.26
645	1.92	14.23	13.65	13.49	14.06
676	2.41	15.73	14.51	15.32	16.61
682	2.20	15.83	14.37	13.90	15.31
716	1.92	15.73	13.45	12.20	12.48
722	2.26	18.13	15.70	12.46	14.39

When feed consumption was adjusted to a weight constant basis the correlations between efficiency and daily gain were high, ranging from 0.77 to 0.89. The correlations between average daily gain and observed gross efficiency, and average daily gain and efficiency after adjusting feed for weight differences found in this study are in close agreement with the correlations reported by Winters and McMahan (1933), and Knapp and Baker (1944). They reported correlations of 0.34 and 0.49 between daily gain and observed gross efficiency of 0.74 and 0.89, respectively, between daily gain and efficiency after adjusting feed for weight differences. Although Knapp and Baker (1944) used the curve of diminishing increment in adjusting for weight differences, the correlations they reported are not essentially different from those found in this study.

According to these data, the best measure of efficiency is the ratio of gain to adjusted feed consumption. Daily gain can also be used to measure efficiency with relatively high accuracy and has advantages in that (1) daily gain or weight for age is usually included in selection indexes, (2) no adjustment is needed for weight differences, (3) selecting the fastest growing animals also selects the most efficient animals, and (4) records of individual feed intake are not needed.

As was previously mentioned, the analysis of variance indicated that rate of gain was relatively constant once the animals were on feed. During the first two periods when the animals were going on feed, the daily gains were below those made during latter periods. According to these data, the first two periods probably should be excluded from the final results since they do not reflect the true abilities of the animals or of the feeds being tested, as the case may be.

Heritability of Feed Consumption

The estimate of heritability should be taken as a rough approximation, since it was obtained from small numbers and varied rather widely from one year to the next. The data suggest that with weight constant, less than 10 percent of the total variance in daily feed consumption is associated with genetic differences. Since the population sampled here was the progeny of fast and slow-gaining bulls, the average genetic effect includes differences larger than expected from random sampling, and is likely to over-estimate the average genetic difference among animals of the same herd.

The data do suggest that progress may be made in selecting for high and low rates of daily feed consumption.

CONCLUSIONS

The investigation seemed to justify the following conclusions:

(1) Feed consumption was influenced by weight. Adjusting feed consumption of each animal to the average weight of its group reduced the total variance 35 percent.

(2) There were differences in feed intake among breeds, sire progenies, and animals within breeds or sire progenies after adjusting for weight differences.

(3) The large variation in feed consumption from period to period indicates that feeding tests in which all animals are not fed in the same periods may contain considerable variation due to period differences and it may not be possible to estimate or control this source of variation statistically.

(4) The ratio of feed to gain is not a satisfactory measure of efficiency unless the animals whose efficiencies are being compared are of equal weight or their feed consumption has been adjusted to a constant weight.

(5) Daily gain appears to be a satisfactory indication of efficiency and seems to be independent of weight.

(6) Daily gain was constant for each animal during its test period and after it was well on feed. All animals were in the

6 - 18 months range of age.

(7) It appears that progress can be expected from selection for high and low rates of daily feed consumption. Heritability of daily feed consumption was estimated at 9.8 percent, but this estimate was subject to considerable sampling error.

SUMMARY

Data collected on weight, feed consumption, and daily gain of 66 steers and 121 bulls were studied by analyses of variance, covariance, correlation, and partial regression. The bulls were of Hereford, Angus, and Shorthorn breeds, and the steers were the offspring of fast and slow gaining bulls that were progeny tested. The feeding tests for the bulls were from 112 to 170 days, and for the steers, approximately 200 days. The bulls and steers were on full feed for the test period, and all animals were fed individually. The first four groups were hand fed and the remaining groups were self fed.

The within-year analyses of variance and covariance of feed consumption and weight showed that weight had a significant influence on feed intake and also that period, sire progeny or breed, group-period interaction, and animal within a sire progeny or breed influenced feed consumption in most years. The components of variance indicated that approximately 35 percent of the total variance of feed consumption was explained by weight.

The correlation between gain and gross efficiency ranged from -0.05 to 0.63, but when efficiency was calculated after adjusting feed consumption to an average weight, the correlation ranged from 0.77 to 0.88, indicating that the ratio of feed to

gain is of little value as a measure of efficiency unless the animals being compared are of equal weight or their feed consumption has been adjusted to a constant weight.

The analysis of variance of daily gain did not show any consistent trend with weight when the first two periods were excluded. The first two periods were significantly different from the remaining periods in some years and indicate that daily gains made during the first 56 days of a feeding test may not be representative of an animal's true ability for a test period of four months or longer.

Heritability of daily feed consumption was estimated by intra-class correlation to be 9.8 percent. The estimate contained considerable sampling error and is likely to overestimate the average genetic differences among animals of the same herd. The data do suggest that progress can be expected from studying for high and low rates of daily gain.

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