SELECTION FOR FEED CONVERSION:
DIRECT AND CORRELATED RESPONSES AND GENETIC PARAMETERS

by

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Ing. Agr., Institute of Technology Zurich, 1974

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Animal Science and Industry

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1976

Approved by:

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Acknowledgements

I would like to thank Dr. Robert R. Schalles for his guidance and assistance during the course of this study and for his great understanding throughout my entire study at Kansas State University.

I also want to thank Dr. Don L. Good, Head of the Dept. of Animal Science and Industry and Dr. John P. Noonan, Assoc. Dean of Graduate School for their financial support and understanding of foreign student exchange.

Special thanks are extended to Dr. J. V. Craig, Dr. G. H. Kiracofe and Dr. G. A. Milliken for serving on my graduate commitee.

I thank my fellow graduate students in animal breeding James Warren and Diane O'Banion for their assistance and friendship.

I'm most endowed to my wife Bernadette for her encouragement and love during our stay in the USA.

Review of Literature

Heritabilities and genetic correlations of calf growth traits

Birth weight is the most important single factor causing calving difficulties (Bellows et al., 1971; Brinks, 1976). Calves that die due to calving difficulties represent a large economic loss. Petty and Cartwright (1966) published weighted averages of all heritability and correlation estimates found in the literature. The weighted heritability estimate for birth weight was 0.44. Brown and Galvez (1969) calculated heritabilities on 789 purebred Hereford and 932 purebred Angus calves born in the years from 1954 to 1964. Sire effects were highly significant and accounted for 20 % and 9.5 % of the total variation of birth weight for Hereford and Angus, respectively. Differences due to years were also highly significant. From a project selecting for yearling weight, Anderson, Fredeen and Weiss (1974) estimated heritabilities by regression of offspring on sire as 0.30 for birth weight, 0.34 for weaning weight and 0.47 for yearling weight.

Birth weight is also related to future growth. Brinks et al.(1964) reported a genetic correlation between birth weight and weaning weight of 0.6 and between birth weight and yearling weight of 0.56. Birth weight was also genetically correlated with gain from birth to weaning (r = 0.46) but not with gain from weaning to 12 months of age (r = 0.07). Petty and Cartwright (1966) reported weighted averages in close agreement with estimates reported by Brinks et al. (1964) except for a genetic correlation of 0.56 between birth weight and postweaning gain.

Koch, Gregory and Cundiff (1974) studied selection responses in three li-lines of Hereford selected for weaning weight, yearling weight or an index of

yearling weight and muscling score. They found genetic correlations between birth weight and postweaning daily gain of 0.58 ± .12 for bulls and 0.40 ± .12 for heifers. Selection for postweaning average daily gain will increase birth weight because of the high genetic correlation. This may be disadventageous because of increased calving difficulties. According to Cundiff (personal communication) selection for postnatal relative growth rate would have a favorable effect on shape of the growth curve increasing response at market weight relatively more than weight at birth or maturity. Relative growth rate was measured as:

$$RGR = \frac{\ln W_{t2} - \ln W_{t1}}{t2 - t1}$$

Correlations between pre- and postweaning growth traits and feed efficiency traits

Lindholm and Stonaker (1957) reported a phenotypic correlation of 0.51 and genetic correlation of 0.05 between weaning weight and feed conversion. Carter and Kincaid (1959) found a lower phenotypic correlation (r = 0.26) and a higher genetic correlation (r = 0.43) between these two traits.

Swinger et al. (1965) published correlations estimated from 480 calves out of 9 different breeding groups. They found genetic correlations of 0.65 between weaning weight and final weight and 1.01 between weaning weight and TDN intake. Brown and Gifford (1962), analysing test performance records of 182 purebred Hereford and 256 purebred Angus bulls, found genetic correlations between final weight and feed consumption of 0.89 and final weight and feed conversion of 0.707.

Efficiency of feed use

The animal that consumes feed only at the maintenance level is completely inefficient as a meat producer, regardless of efficiency or inefficiency of main tenance.

Brown and Gifford (1962) clearly demonstrated the variation in intake between animals. They looked at feed consumption while holding the effects of breed from which the animal came, age on test and weight on test constant during a 154 day test period. Feed consumption ranged from 1600 to 4000 lb. reflecting differences in feed consumption among cattle of the same general size. Heritability estimate for feed consumption was 0.76. In a later study Brown and Gacula (1964) estimated heritabilities on the same data using a regression technique. The estimate was 0.43 ± .18 and in close agreement with estimates of 0.38 by England et al. (1961) and the estimate of 0.45 ± .46 and 0.38 ± .36 reported by Swinger (1961) for daily TDN intake. Koch et al. (1963) found a slightly higher heritability estimate of 0.64 for feed consumption during a 168 day test period. Bogart and England (1971) estimated a heritability of 0.38 ± .15 for daily feed intake by regression of offspring on midparent. They concluded that variation of daily feed consumed is partly under genetic control.

Taylor, Watson and Young (1962) have shown the nutritive value per unit of ration declines progressively as the level of feed intake increses. This reduction in nutritive value is the result of increased waste of energy at certain stages of energy utilization.

Brody (1945), Blaxter (1962) and Reid (1962) showed the utilization of metabolic energy is more efficient at stages below maintenance than above. Therefore on plane of nutrition close to the maintenance level net energy is used

more efficiently than on higher planes of nutrition.

Little variation in the ability to digest nutrients exists between ruminant species, between breeds and within breeds. Blaxter and Wainman (1964) compared the ability of cattle and sheep to digest nutrients. Six diets were given at the maintenance level. No significant differences in efficiency of digestion could be found between those two ruminant species. Holter and Reid (1959) found a coefficient of variation of 2.2 % for digestive ability of animals within the same breed of cattle.

Flatt and Coppock (1963) showed the basal metabolism of cattle of the same size varies about the mean with a coefficient of variation of $\pm$ 10 %. Blaxter and Wainman (1966) compared the fasting heat production. Aberdeen Angus steers had a significant 18.3 kcal less heat produced per unit of metabolic size (wt$^{.75}$) than Ayrshire. Vercoe (1970), using Brahmans, Africander and Hereford crosses reported a coefficient of variation of 13.2 % in fasting heat production.

Body composition of an animal changes with increasing stage of maturity. Water content decreases and fat content increases sharply while protein and ash content decrease slightly. Feed required to lay down fat is seven times greater than to lay down protein tissue (Blaxter, 1964). Wagner (1972) hypothesized that different types of cattle (big, medium and small) would be about equally efficient at equal points in the growth curve.

Lipsey, Dikeman and Riley (1975) compared steers by Maine-Anjou, Gelbvieh, Hereford and Angus sires from Hereford-Angus crossbred cows, fed to the same efficiency end point. Each steer was slaughtered when its biweekly energy efficiency exceeded 8.0 Mcal net energy for production (NEp) per kg gain. Maine-Anjou and Gelbvieh sired steers required less total energy per kg gain than the Hereford x Angus steers to reach the same NEp efficiency end point. Maine Anjou

and Gelbvieh sired steers also were 91 kg heavier and gained 0.14 kg more per day than the Hereford and Angus sired steers.

Measurements of efficiency of feed use

Among animal husbandmen the most common measurement of efficiency of feed use is the ratio of either feed consumed per gain (feed conversion) or gain per feed consumed (feed efficiency).

Weil (1962) mentioned three reasons to justify the use of a ratio: (1) the two items considered should increase or decrease together in a linear fashion, (2) the regression line for the two variables should intercept at zero, and (3) the variance of the variable should increase with the increasing magnitude of the variables.

Koch et al. (1963) rejected a linear relationship between gain and feed consumption. They concluded that a quadratic regression would describe the relationship better. Different regression were used to describe efficiency of feed use.

1. Feed consumption was adjusted for gain and mid weight. Four partial regressions i.e. both first and second degree of feed consumption on gain and feed consumption on mid weight were computed simultaneously.

2. The second measure of efficiency of feed use was gain adjusted for differences in feed consumption after first adjusting feed consumption for mid weight, which should remove the variation in maintenance. The quadratic effect of feed consumption was significant but accounted for only 3 % of the total variation.

3. The third measurement of efficiency was the ratio of gain to feed consumption, where feed consumption was adjusted for differences in mid weight.

Gain adjusted for differences in feed consumption and the ratio of gain

over feed consumption adjusted for maintenance were highly correlated. They concluded that the ratio would be a poor measure of efficiency at a level of nutrition close to maintenance or if feed consumption and gain varied over a wide enough range so that the curvilinearity would be more important.

The heritability (Koch et al., 1963) for feed consumption adjusted for gain and mid weight estimated by half sib covariances was 0.28 ± .11, for gain adjusted for feed consumed after correcting for maintenance 0.62 ± .12 and for the ratio gain to feed consumption 0.36 ± .10. Several heritability estimates for feed efficiency were found in the literature. By using half sib correlations Brown and Gifford (1962) estimated a value of 0.8; Carter and Kincaid (1959), 0.99; Dawson et al. (1955), 0.03; Knapp and Nordskog (1946), 0.75; and Shelby et al. (1950), 0.32. Carter and Kincaid (1959) estimated a heritability of 0.35 by sire-offspring regression. Knapp and Nordskog (1946) found a heritability of 0.48 using the same method.

Correlations between efficiency of feed use, average daily gain and feed consumption

Several researchers felt suspicious about the high correlation between the ratio feed consumed to gain it's denominator gain. Tanner (1949) showed "ratio standards" which express physiological functions as per weight or per surface area can be misleading. After comparing "ratio and linear regression standards" he concluded that the regression describes the relationship better. Sutherland (1965), although concluding that animal scientists never use "ratio standards", stated that the ratio of feed consumption to weight gain is a valid estimate of efficiency of feed use and also that the correlation between the ratio and it's numerator or denominator describes the relationship well. Knapp and Baker

(1944) found the correlation between rate and efficiency of gain is smaller in populations where the test period is constant in length.

Magee (1962), analysing swine data, found pigs which ate the most tended to be the least efficient. From 80 boars raised in six groups he found a phenotypic correlation between feed consumption and feed efficiency of -.37, which was highly significant. The genetic correlation was so close to zero that he concluded feed efficiency cannot be improved by selection for appetite. One reason for this unfavorable relationship between daily feed consumption and feed efficiency may have been the curvilinear relationship, but he could not find any indication for it in his data. Maintenance differences were not taken into account, although the initial and final weight varied. Brown and Gifford (1962) found a genetic correlation between feed conversion and feed consumption of 0.709 and Bogart and England (1971) reported a value of 0.269. Both authors did not adjust feed used for maintenance. Koch et al. (1963) estimated a genetic correlation of 0.04. There seems to be no agreement in the literature about the relationship of these two variables.

Pearson (1897) derived an equation to predict the correlation between x_1 and the ratio x_1 to x_2 using the simple correlation between x_1 and x_2 and the coefficients of variation. Sutherland (1965) also gives a formula to predict the genetic correlation between x_1 and the ratio x_1 to x_2. By this theoretical approach he reached the conclusion that the correlation between gain and feed conversion cannot be positive while the correlation between gain and feed consumption is negative. Most authors agree on a moderate to high correlation between feed consumption and gain. Bogart and England (1971) reported a phenotypic correlation of 0.35, Koch et al. (1963) reported a phenotypic correlation

of 0.62 and a genetic correlation of 0.64. Brown and Gifford (1962) found a phenotypic correlation of 0.39 and Magee (1962) found on swine data phenotypic correlations of 0.79 and 0.74. For positive values of the correlation between feed consumption and gain, and the coefficient of variation larger than that of feed consumption (as it usually is), Sutherland (1965) reported a theoretical range for the correlation between gain and feed conversion of -.5 to 0.5. Similar values hold for genetic correlations. Magee (1962) found a fairly high correlation between gain and feed efficiency. Similar results were reported by Brown and Gifford (1962) (r_g = -.34) and Bogart and England (1971) (r_p = -.70) both using feed conversion as a measurement of efficiency. Lickley (1960) reported phenotypic correlations between gain and feed conversion of -.45 when adjusted for initial weight and -.26 when not adjusted.

Fitzhugh and Cartwright (1971) reported an experiment in which variation in feed consumption among steers was eliminated so that differences in weight gain would show the variation in feed efficiency. The phenotypic correlation between weekly gain and feed efficiency was 0.97 $\pm$ .02 and the genetic correlation 1.00 $\pm$ .0. This shows that weight gain under constant feed intake is a good measurement of efficiency of feed use.

Backfat thickness and loin eye area measurements on live animals

Cox (1964) reported a heritability for backfat thickness in swine of 0.25. The measurements were taken at a constant age using the probe technique.

Dinkel and Busch (1973) studied the relationship among beef growth traits and carcass characteristics. Fat thickness was an average of three measurements taken from an acetate tracing of 12th. rib. Rib eye area was a planimeter measurement of the acetate tracing of the longissimus muscle. Heritability for

backfat thickness was 0.57 and for rib eye area 0.25. The genetic correlation between these two traits was -.59. Rib eye area was highly positive correlated with weaning weight, daily gain and final weight. Backfat thickness was highly negative correlated with weaning weight (r_g = - 1.00). Daily gain and final weight were negatively correlated with fat thickness (r_g = -.25 respectively -.56).

Davis, Temple and McCormick (1966) compared ultrasonic estimates of rib eye area and fat thickness in cattle with actual carcass data. The correlation between the ultrasonic estimate and carcass measurement of rib eye area was 0.6, between the ultrasonic estimate and carcass fat thickness 0.7.

Summary

Data from a selection experiment for feed conversion using a control population were analysed to calculate direct and correlated responses. Least squares estimates of line differences (selected vs. control) for the final year showed a cumulative selection response of 0.23 lb. less feed per lb. of gain. Associated with this response was a decrease in birth and weaning weight. Average daily gain on test, average daily gain from weaning to yearling, and the relative growth rate during this period have increased. Selection for feed efficiency tended to lower yearling height but weight was not changed.

Loin eye area and backfat thickness were used as indicator of the stage of physiological maturity. No change in these traits were found due to selection.

A realized heritability of 0.61 has been calculated for feed conversion adjusted for maintenance. Heritabilities were also estimated by half sib correlations. The values estimated on the performance of 257 bulls were: birth weight, 0.42; 205 day weight, 0.31; 365 day weight, 0.41; average daily gain from birth to weaning, 0.37; average daily gain on 140 day postweaning test, 0.30; yearling height at shoulder, 0.56; total feed consumption on test, 0.40; feed conversion, 0.23; feed conversion adjusted for maintenance, 0.24; loin eye area, 0.11; and backfat thickness, 0.18. Heritabilities, calculated for bulls and heifers combined (n = 504) using the same method, were: Birth weight, 0.29; yearling height, 0.66; loin eye area, 0.15 and backfat thickness, 0.12.

Introduction

With increasing cost of energy one gets more concerned about efficient use. There has always been some natural selection for efficiency. Animals which were unable to convert the available feed efficiently failed to reproduce or had a reduced reproduction rate.

Today the cattleman can control environmental and genetic characteristics of his herd. Selection for feed conversion alone may not be the most economical, but it brings the fastest change in this trait. Because selection for feed conversion is extremely costly it may be advantageous to select for complimentarity and crossing the complimentary genotypes.

This experiment was initiated to study the genetic changes which occur in a herd selected for efficient feed conversion. This thesis is concerned with the evaluation of realized selection responses after seven years of selection.

Experimental Procedure

Performance data were collected on 257 bull calves and 247 heifer calves from the Polled Hereford herd at Kansas State University from 1969 through 1975. This herd was initiated in 1967 when Polled Hereford breeders from Kansas, Oklahoma, Missouri, Illinois and Pennsylvania donated cattle from 34 herds. These cows were used to build the Polled Hereford herd to it's present size of about 160 cows in the selection herd and 73 in the control herd.

For the 1971 breeding season cows were randomly assigned to either the selection or control line. Bulls used in the selection group were born in 1969 and 1970 and had the best feed conversion during a 140 day test period. Since 1969 two bulls were selected annually for the selection herd. They were used in the breeding herd for two consecutive years.

Bulls for the control herd were randomly selected within herd and remained in the herd 6 years or as long as possible. Since 1970 both lines have been closed and no other breeding material has been introduced. To reduce the increase of inbreeding, least related matings have been used. Cows were maintained on native pasture all year and different levels of energy and protein supplements have been fed during the winter (Davis 1974).

Cows were bred to calve in March and April, and calves were weaned at approximately 200 days age. Following a 3 to 4 week weaning period bulls were put on a 140 day individually fed performance test using the ration given in table 1. At the end of the test, 2 bulls were selected for the selection herd. The criterion selected for was feed conversion (F/G_{adj}.) adjusted for (mid weight)$^{3/4}$ and age on test. Partial regression coefficients have been computed every year using all previous data. These partial regression coeffi-

cients were used to adjust each individuals F/G ratio to an average age and (mid weight)$^{3/4}$.

TABLE 1. RATION FED DURING THE 140 DAY PERFORMANCE TEST

Ingredient	%
Prairie hay	25.0
Dehy Alfalfa	15.0
Corn	43.0
Soybean meal	12.5
Molasses	4.0
Salt	0.5

Heifers were group fed. Monthly weights were taken on the bulls and the heifers were weighed bimonthly. No selection for feed conversion has been performed on the heifers. Essentially all heifers have been kept to build up the herd and for replacement. Culling was done according to the following criteria: (1) non pregnant at the end of the breeding season, (2) severe structural damages, and (3) horned.

The measurements of growth, feed consumption and feed utilization are defined as follows:

BW	= birth weight
205 WT	= adjusted 205 day weight
365 WT	= adjusted 365 day weight

ADG (B-W)   = average daily gain from birth to weaning

RGR (B-W)   = relative growth rate from birth to weaning

ADG (W-Y)   = average daily gain from weaning to yearling

ADG (T)   = average daily gain on 140 day performance test

RGR (W-Y)   = relative growth rate from weaning to yearling

Y HT   = yearling height measured at the shoulder

FC   = total feed consumption during the 140 day performance test

$F/G_{adj.}$ = total feed consumption divided by gain on test, corrected to

                   a constant (mid weight)$^{3/4}$ and age

F/G   = total feed consumption divided by gain on test, not

                   adjusted for maintenance, but for age on test and weight

                   on test

LEA   = loin eye area

BF   = backfat thickness

Adjusted 205 day weight and 365 day weight were calculated using the procedure recommended by the Beef Improvement Federation (1974).

Average daily gain from birth to weaning equals

$$ADG\ (B\text{-}W) = \frac{205\ WT - BW}{205}$$

and average daily gain from weaning to yearling

$$ADG\ (W\text{-}Y) = \left[365\ WT - \left(\frac{205\ WT}{age\ of\ dam\ adj.} \right) \right] / 160$$

205 WT has been divided by the age of dam adjusted. Thereby, average daily gain from weaning to yearling remains adjusted for the age of dam effect.

Relative growth rate as reported by Fitzhugh and Taylor (1971) and Cundiff (personal communication) is the ratio of average daily gain to the average weight over the period tested.

The formula for relative growth rate from birth to weaning is

$$\text{RGR (B-W)} = \frac{\text{ADG (B-W)}}{(\text{BW} + 205 \text{ WT})/2}$$

relative growth rate from weaning to yearling age is

$$\text{RGR (W-Y)} = \frac{\text{ADG (W-Y)}}{(205 \text{ WT} + 365 \text{ WT})/2}$$

Loin eye area and backfat thickness were measured by a Scanogram at about yearling age. The results were adjusted to a constant weight and age of measurement.

The method used to calculate direct selection response was published by Newmann, Rahmefeld and Fredeen (1973) and is identical to the method used by Turner and Young (1969). The nomenclature used is as follows:

Contemporary group (CG)   : Mean of calf group of the same sex born in the same line and year

Individual's deviation (ID) : The individual's deviation from his contemporary group

Mean accumulated

selection differential (MAS) : The mean individual accumulative selection differential (see below) of the parents of a contemporary group weighted by the number of offsprings per parents in this particular contemporary group

Individual's accumulated

selection differential (IAS) : The individual's deviation from the mean plus the mean accumulated selection differential of the parents of his contemporary group

This mean accumulated selection differential was used to calculate a realized heritability. Falconer (1960) called the ratio of selection response to accumulated selection differential a measure of the true heritability.

Correlated responses to selection for feed conversion were analysed accorcing to the following model:

$$Y_{ijk} = \mu + Year_i + Herd_j + (Year \times Herd)_{ij} + \varepsilon_{ijk}$$

Heritabilities have been estimated only for bulls because a preliminary analysis showed significant sex by year interactions in 365 day weight and ADG and RGR from weaning to yearling. This was primarily because the nutrition level for heifers has been drastically changed over the years. Half sib correlations have been analysed according to the model:

$$Y_{ij} = \mu + Year_i + Sire_j + \varepsilon_{ij}$$

Birth weight has been corrected for age of dam, winter nutrition of dam and

birth month. Preweaning growth characters and 205 day weight have been correc-
ted for birth weight, winter nutrition of the dam and age of dam. Postweaning
growth traits and F/G are corrected for weight on test and age on test.
$F/G_{adj.}$ is corrected for age on test and (mid weight)$^{3/4}$. Loin eye area, back-
fat thickness and yearling height were adjusted to a constant weight and age.

Results and Discussion

The individual's deviation from the herd's average feed conversion was calculated within years. In 1969, 1970 and 1971 selection and control line were a single herd. Therefore individual deviation have been calculated as deviations from the entire herd. In 1972 these two lines were completely separated and the individual deviations are the differences between the selection line mean and the individual's performance. Table 2 shows means of the contemporary groups from 1969 to 1975. Year to year fluctuations are quite large. Individual deviations of the selected bulls tend to decrease.

From 1969 to 1971 the mean accumulated selection differential of the parents was zero, because they were unselected. It is also zero for bull 235, because he is selected from the control herd. In 1974 offsprings of selected bulls start calving, giving an increase in the mean accumulated selection differential from the dam side.

The actual selection intensity (table 3) did not reach the theoretical value given for small populations by Becker (1975). This could be due to deviations from normal distribution or inaccurate selection.

Table 4 shows least square means and differences in feed conversion between selection and control herd. These are genetic differences, because both herds are kept under the same environment and no genetic changes are assumed to have taken place in the control herd. Using selected bulls improved feed conversion by about 0.35 lb. per lb. gain. With an average 400 lb. gain on test this is 140 lb. less feed consumed on the 140 day test. The regression of least square means on years indicates a decrease per year of 0.141 $\pm$ .567 lb. feed per lb. of gain in the selection line and 0.067 $\pm$ .551 in the control line (figure 1).

TABLE 2. CONTEMPORARY GROUP MEAN, SELECTION DIFFERENTIALS AND
ACCUMULATED SELECTION DIFFERENTIALS

Year	Contemporary group mean	Bulls identifica- tion number	Individuals deviation	Mean accumu- lated selection differential	Individuals accumulated se- lection differen- tial
1969	6.845 + 0.41	907	-.409	0	-.409
		925	-.703	0	-.703
1970	6.686 + 0.48	020	-1.027	0	-1.027
		063	- .559	0	- .559
1971	6.087 + 0.50	125	-.628	0	-.628
		136	-.514	0	-.514
1972	5.138 + 0.40	230	-.498	-.346	-.862
		235	-.601	0	-.601
1973	5.884 + 0.47	324	-.468	-.361	- .829
		3111	-.668	-.361	-1.029
1974	6.350 + 0.52	4150	-.664	-.331	-.995
		403	-.328	-.331	-.659
1975	5.773 + 0.40	542	-.572	-.377	-.949
		529	-.303	-.377	-.680

TABLE 3. ACTUAL AND THEORETICAL SELECTION INTENSITY

Year	Number of bulls	Actual selection intensity	Theoretical selection intensity
1969	20	1.199	1.638
1970	23	1.599	1.705
1971	33	0.993	1.872
1972	12	0.671	1.372
1973	27	1.126	1.798
1974	36	0.952	1.911
1975	36	1.105	1.911

TABLE 4. LINE AVERAGES AND DIFFERENCES IN FEED CONVERSION BETWEEN SELECTION AND CONTROL LINE

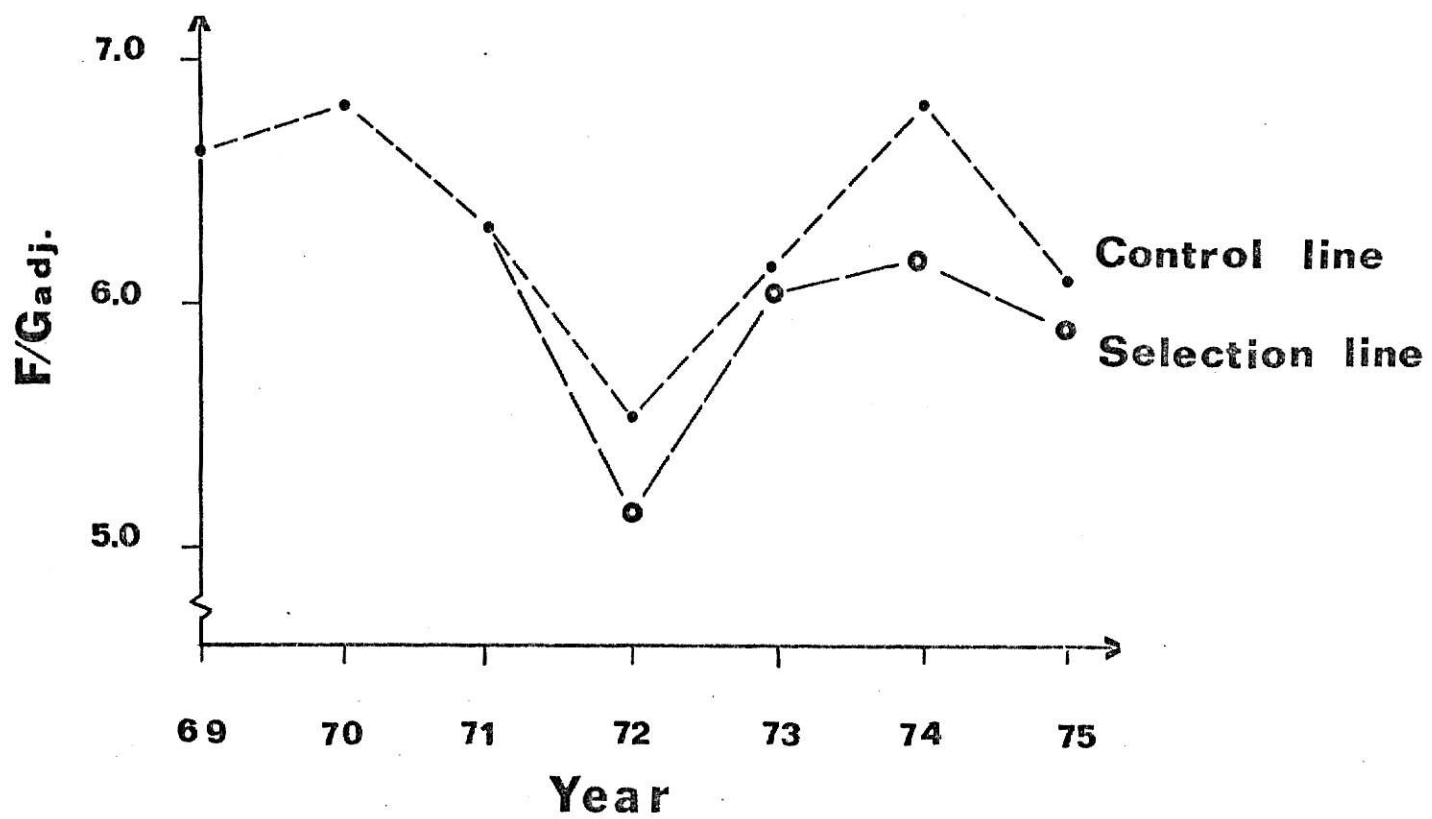| Year	No. of bulls	Selection line mean	No. of bulls	Control line mean	Response to selection for F/G_{adj}
1969			20	6.64 ± .21	
1970			23	6.83 ± .15	
1971			33	6.33 ± .13	
1972	12	5.12 ± .22	25	5.53 ± .15	- .41 ± .23
1973	27	6.03 ± .14	12	6.10 ± .21	- .07 ± .21
1974	36	6.16 ± .12	27	6.82 ± .14	- .66 ± .14
1975	36	5.87 ± .13	21	6.10 ± .15	- .23 ± .16

Figure 1. Time trend in feed conversion adjusted for maintenance and change by selection.

A realized heritability of 0.61 was calculated. A large standard error is attached to it, because only two generations of selection have been carried out.

Birth weight and 205 day weight have been lowered by selection for feed conversion (table 5). Calves in the selection line were lighter at birth than calves in the control line. In 1972 the difference was 5.25 lb. ($P < 0.05$) for heifers and in 1974, 4.16 lb. ($P < 0.05$) for bulls. The decrease in birth weight and 205 day weight was consistent for both sexes. Yearling weight was not changed by selection for feed conversion. Changes in shape of the growth curve from birth to yearling are shown for both sexes in figure 2. Average daily gain from birth to weaning tended to be decreased ($P < 0.10$). Adjusted weaning weight was significantly decreased and average daily gain from weaning to yearling was significantly increased. Both lines had the same yearling weight. An analysis of ADG on test by 4 week intervals showed control line calves to start out with higher gain per day (table 6). Toward the end of the test, however, calves in the selection line gained more rapidly than control line calves. No inference could be made about the shape of the growth curve beyond yearling.

The decrease in 205 day weight also suggests that by adjusting feed per gain to a constant (mid weight)$^{3/4}$, does not remove all the variation due to maintenance. Examination of individual's performances suggests that selection may have been on two independent traits. Bulls who grew slow during the first half of the test and fast during of the last part of the test were favored because of lower maintenance requirement than was adjusted for by using (mid weight)$^{3/4}$. Bulls which gained fast throughout the test, or much faster during the early part of the test than at the end were selected either because

TABLE 5. CORRELATED RESPONSES; AVERAGES AND DIFFERENCES BETWEEN SELECTION AND CONTROL LINE

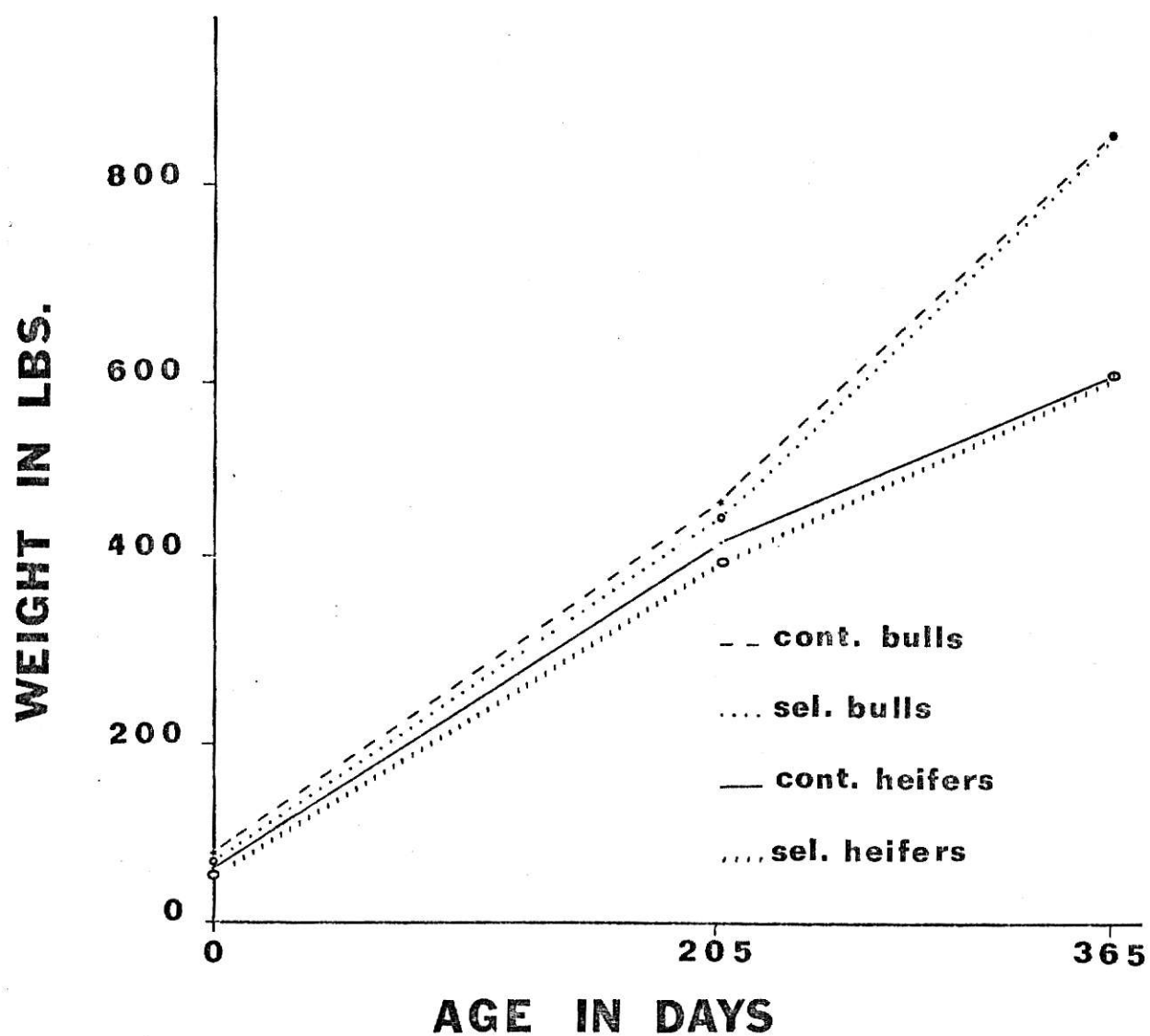| Year		1972			1973			1974			1975		
Trait	Sex	Sel.	Cont.	Diff.	Sel.	Cont.	Diff.	Sel.	Cont.	Diff.	Sel.	Cont.	Diff.
BW	B	70.98	71.34	-.36	68.68	71.78	-3.1	73.20	77.36	-4.16*	75.27	78.89	-3.62
BW	H	64.75	70.00	-5.25*	65.19	67.69	-2.5	70.75	72.21	-1.46	72.30	74.28	-1.98
205 WT	B	486.51	461.23	25.28	462.45	503.74	-41.29*	439.05	450.47	-11.42	411.85	441.91	-30.06*
205 WT	H	418.68	446.33	-27.65	414.68	439.92	-25.24	424.75	429.08	-4.33	392.98	403.84	-10.86
365 WT	B	896.45	853.96	42.49	872.92	909.13	-36.21	893.89	887.82	6.07	843.88	851.67	-7.79
365 WT	H	595.43	608.32	-12.89	631.10	641.16	-10.06	597.92	604.05	-6.13	616.91	589.01	27.9
ADG (B-W)	B	1.883	1.776	0.107	1.812	1.919	-.107	1.733	1.784	-.051	1.641	1.743	-.102
ADG (B-W)	H	1.621	1.709	-.088	1.591	1.613	-.022	1.695	1.680	0.015	1.562	1.547	0.015
RGR (B-W)	B	.00703	.00698	-.00005	.00709	.00703	-.00006	.00690	.00683	.00007	.00671	.00674	.00003
RGR (B-W)	H	.00695	.00697	-.00002	.00700	.00676	.00024	.00694	.00684	.00010	.00673	.00661	.00012
ADG (W-Y)	B	2.680	2.552	0.128	2.758	2.559	0.199	3.077	2.754	0.323**	2.860	2.637	0.223*
ADG (W-Y)	H	1.323	1.148	0.175	1.532	1.258	0.274	1.278	1.121	0.157	1.583	1.232	0.351**
ADG (T)	B	3.006	2.840	0.166	3.062	2.992	0.070	2.891	2.690	0.201*	2.934	2.872	0.062
RGR (W-Y)	B	.00389	.00391	-.00002	.00415	.00364	.00051**	.00462	.00412	.00050**	.00457	.00409	.00048**
RGR (W-Y)	H	.00264	.00219	.00045*	.00293	.00238	.00010	.00249	.00217	.00032*	.00313	.00249	.00064**
Y HT	B				42.136	43.383	-1.247	42.539	42.537	0.002	41.951	42.427	-.476
Y HT	H				37.600	38.510	-.910	38.020	39.358	-1.338	39.925	39.828	0.097
FC	B	2209.9	2147.5	62.4	2573.7	2615.8	-42.1	2546.7	2587.1	-40.4	2346.7	2400.9	-54.2
LEA	B	9.607	9.532	0.075	11.559	12.263	-.704	11.281	11.085	0.176	11.228	11.018	0.210
LEA	H	6.314	6.888	-.574	7.910	8.392	-.482	7.667	7.792	-.125	7.637	7.595	0.042
BF	B	0.241	0.234	0.007	0.196	0.179	0.017	0.359	0.378	-.019	0.275	0.259	0.016
BF	H	0.125	0.120	0.005	0.113	0.122	-.09	0.127	0.167	-.040	0.147	0.173	-.026

* P<.05
** P<.01

Figure 2. Shape of the growth curve in selection and control line according to sex.

of superior efficiency or because of the high correlation between ADG on test and feed conversion. Koch et al. (1963) reported that when the quadratic effect of days-on-test on weight is significant (as it was here), it would be advantageous to adjust not only for (mid weight)$^{3/4}$ but make adjustments for differences in weight at several intervals. I fitted a quadratic regression, 28 day weights on days-on-test and on (days-on-test)^2 for each animal. The area under the regression curve divided by 140 was the "average weight maintained" by each bull during the 140 day test period (appendix A). Differences between (mid weight)$^{3/4}$ and (average weight)$^{3/4}$ were rather consistent within years (table 7). In 1969, 1973, 1974 and 1975 (average weight)$^{3/4}$ was larger than (mid weight)$^{3/4}$ for most animals suggesting faster growth at the beginning of the test. In 1971 and 1972 the growth of most bulls was faster at the end of the test than at the beginning. I concluded these year to year variation to be primarily an environmental effect on the shape of the growth curve and the deviations within years between individuals included genetic effects.

No significant changes in backfat thickness and loin eye area resulted from selection for F/G_{adj}, although it is expected that in future generations the animals in the selection line will be less fat, because from an energetic standpoint (Blaxter 1964) it requires seven times more energy to lay down fat, than protein tissue.

Total feed consumption has not been significantly changed. This agrees well with the genetic correlations between F/G_{adj} and feed consumption, which was found to be near zero.

Yearling height was not significantly effected but was generally lower

TABLE 6. CHANGES IN AVERAGE DAILY GAIN DURING THE 140 DAY PERFORMANCE TEST

Year	1972		1973		1974 -		1975	
Days on test	Sel.	Contr.	Sel.	Contr.	Sel.	Contr.	Sel.	Contr.
0	2.17	2.22	3.68	3.99	4.04	4.20	3.53	3.61
28	2.50	2.43	3.44	3.63	3.56	3.64	3.27	3.32
56	2.82	2.64	3.20	3.28	3.09	3.09	3.00	3.02
84	3.15	2.84	2.96	2.93	2.61	2.54	2.74	2.73
112	3.47	3.05	2.72	2.57	2.14	1.99	2.48	2.43
140	3.80	3.26	2.49	2.22	1.66	1.44	2.22	2.14

TABLE 7. NUMBER OF CALVES HAVING POSITIVE OR NEGATIVE DIFFERENCES BETWEEN (MID WEIGHT)$^{3/4}$ AND (AVERAGE WEIGHT)$^{3/4}$

Year	positive	negative
1969	0	21
1970	15	10
1971	31	2
1972	33	4
1973	2	39
1974	1	71
1975	0	54

in the selection line. The genetic correlation between $F/G_{adj.}$ and yearling
height indicates a low negative genetic relationship ($r = -.23$).

Heritability estimates of 14 performance traits are given in table 8.
Heritability was for birth weight 0.42. Similar estimates can be found in the
literature (Petty and Cartwright , 1966 and Anderson et al., 1974). Age of
dam, birth month and winter nutrition of the cow affected birth weight signi-
ficantly. This is in agreement with Davis (1974) who analysed the influence of
winter nutrition in this herd.

Weaning weight and average daily gain from birth to weaning is largely
affected by the maternal ability of the dam and the percentage of genetic varia-
tion is lower than for birth weight or 365 day weight. Heritabilities found in
this study were 0.31 for 205 day weight and 0.37 for ADG from birth to weaning.
Petty and Cartwright (1966) reported 0.28 for weaning weight and Lasley (1972)
0.25.

The heritability estimate for 365 day weight was 0.41 in this study, which
is lower than the weighted average reported by Petty and Cartwright (1966) for
final feedlot weight ($h^2 = 0.58$) and Anderson et al. (1974) for yearling weight
($h^2 = 0.47$).

Average daily gain from 205 to 365 days of age and average daily gain on
test measure essentially the same. Heritability estimates for both traits were
0.30. These estimates are lower than those reported by most other researchers.

Selection for postweaning relative growth rate has been proposed by
Fitzhugh and Taylor (1971) and Cundiff (personal communication) to increase
market weight relatively more than birth or mature weight. A heritability of
0.65 was estimated for relative growth rate on test.

Yearling height at the shoulder is a measurement of body size and gained

TABLE 8. HERITABILITIES (ON DIAGONAL) AND GENETIC CORRELATIONS (BELOW DIAGONAL) FOR GROWTH AND EFFICIENCY TRAITS[e]

	BW	205 WT	365 WT	ADG(B-W)	ADG(W-Y)	ADG(T)	Y HT	FC	F/G$_{adj.}$	F/G	LEA	BF
BW	d 0.42±.21											
205 WT	a 0.96±.81	0.31±.18										
365 WT	b 0.77±.44	0.64±.26	0.41±.21									
ADG(B-W)a	0.26±.22	0.99±.01	0.60±.27	0.37±.20								
ADG(W-Y)b	0.87±.22	0.45±.44	0.97±.03	0.20±.42	0.30±.18							
ADG(T)	b 0.80±.25	0.24±.55	0.94±.05	0.00±.54	0.88±.10	0.30±.18						
HT	c 0.22±.19	0.09±.28	0.52±.30	-.05±.39	0.39±.31	0.48±.34	0.56±.31					
FC	b 0.85±.26	0.09±.16	0.59±.23	-.22±.46	0.36±.29	0.56±.24	0.11±.24	0.40±.20				
F/G$_{adj.}$	b -.15±.41	0.08±.62	-.68±.24	0.05±.51	-.84±.19	-.53±.31	-.23±.11	0.06±.43	0.23±.16			
F/G	b 0.05±.41	0.11±.62	-.72±.33	0.06±.50	-.78±.21	-.39±.37	-.44±.19	0.17±.41	0.93±.04	0.24±.16		
LEA	c 0.68±.50	0.31±.29	0.73±.44	-.32±2.2	0.93±.43	0.77±.46	0.01±1.6	0.16±.54	-1.08±.52	-1.05±.52	0.11±.13	
BF	c -.26±.40	0.14±.75	-.07±.15	0.06±.63	-.12±.45	-.20±.51	-.54±.22	0.37±.51	-.05±.54	0.02±.51	-.03±.52	0.18±.15

a   adjusted for age of dam, winter nutrition of dam and birth weight
b   adjusted for age on test and weight on test
c   adjusted for age and weight at anscan
d   adjusted for age of dam, winter nutrition of dam and birth month
e   all traits had 257 observations except yearling height which had 154

in importance during the last few years by the search for growthier animals. Pircher (1969) reported a range of 0.5 to 0.7 for the heritability of this measurement. Our estimate of 0.56 for bulls and 0.66 for a pooled estimate of heifers and bulls lies well within these limits.

Two measurements of efficiency of feed use (F/G and $F/G_{adj.}$) have been applied in this study. The genetic correlation of 0.93 between them suggests that the adjustment for maintenance does not change much. A heritability of 0.24 has been computed for feed conversion and 0.23 adjusted for maintenance. This is lower than our realized heritability of 0.61. Knapp and Nordskog (1946) reported 0.48; Dawson et al. (1955), 0.32; Carter and Kincaid (1959), 0.99; Brown and Gifford (1962), 0.8; and Pirchner (1969) give lower and upper limits of 0.30 to 0.40.

Loin eye area (LEA) and backfat thickness (BF) measurements on the live animal involve more measuring errors than the ones taken on the carcass. This may explain the low heritabilities for LEA (h^2 = 0.12) and for BF (h^2 = 0.15) compared to estimates obtained from carcass data.

Genetic correlations are primarily the result of pleiotropy and linkage. In part-whole relationships, as between birth weight, 205 day weight and 365 day weight, high positive genetic correlation have been calculated (table 8). Postweaning average daily gain was also highly correlated with all other weight measurements. Average daily gain from birth to weaning had a low genetic correlation with birth weight (r = 0.26), ADG from weaning to yearling (r = 0.20), ADG on test (r = 0.0) and yearling height (r = -.05).

Loin eye area and growth measurements were generally positively correlated, except for the correlation between ADG from birth to weaning and LEA, where the estimated value was -.32. Backfat thickness and growth characters were negative-

ly correlated. Exceptions from this were the correlations between ADG birth to weaning and BF (r = 0.06) and 205 day weight and BF (r = 0.14). These relationships agree well with correlations given by Dinkel and Busch (1973) who reported fat thickness measured on the carcass to be negatively correlated with postweaning average daily gain (r = -.25) and final weight (r = -.56). LEA was highly positive correlated with postweaning daily gain (r = 0.49) and final weight (r = 0.54).

Feed consumption was positively correlated with weights at all stages and also with ADG on test (r = 0.56). Similar results found Koch et al. (1963) reporting a genetic correlation of 0.64 between average daily gain on test and feed consumption.

$F/G_{adj.}$ was negatively correlated with birth weight (r = -.15) as well as 365 day weight (r = -.68) but birth weight was decreased by selection for feed conversion. On the other hand 205 day weight is positively correlated with $F/G_{adj.}$ and decreased with selection. In this early stage of the selection experiment the biggest correlated response seems to be a decreased 205 day weight. Weight at 205 days is positively correlated with all other weight measurements. Therefore, there seems to exist an antagonistic effect, causing 365 day weight to stay constant and birth weight to decrease.

The correlation between ADG on test and feed conversion is of special interest, because we correlate a ratio with its denominator. Sutherland (1965) gives an equation to predict this correlation using heritabilities and coefficients of variation of ADG on test and feed consumption and the simple correlation between them. The predicted genetic correlation in this study was -.56, estimated values were -.39 by not adjusting for maintenance and -.53 when feed

conversion was adjusted for maintenance. Correlations found in the literature agree on a negative relationship between average daily gain on test and F/G ratio. Brown and Gifford (1962) reported a genetic correlation of -.34 and Bogart and England (1971) a phenotypic correlation of -.70. When we adjusted feed conversion for maintenance we observe a higher negative genetic correlation. The partial regression of F/G (not adjusted for maintenance) on (mid weight)$^{3/4}$ is positive (b = 0.0233), suggesting high (mid weight)$^{3/4}$ to increase feed required per unit of gain. ADG on test and (mid weight)$^{3/4}$ are positively correlated (r 0.97 $\pm$ .57). If we correct F/G to a constant (mid weight)$^{3/4}$, animals above an average (mid weight)$^{3/4}$ will lower their F/G$_{adj.}$ relative to their F/G and animals below the average will increase it. From this we can conclude that the correlation between ADG on test and F/G$_{adj.}$ has a higher absolute value than the correlation between ADG on test and F/G.

Lickley (1960) reported phenotypic correlations between gain and feed conversion adjusted for initial weight instead of adjusting for (mid weight)$^{3/4}$. The correlations reported were -.45 when adjusted and -.26 when not adjusted. Realized correlated response in our study support a negative relationship between ADG on test and F/G$_{adj.}$, but no inference could be made about the magnitude of this value.

The correlation between feed consumption and F/G by not adjusting for maintenance is expected to be positive, because higher feed consumption is primarily attributed to higher maintenance requirements. When we adjust for maintenance the correlation is 0.06, suggesting feed conversion can not be improved by selection for feed consumption. By selection for F/G$_{adj.}$, feed consumption has been slightly (nonsignificantly) decreased, which suggests a slight

positive relationship. Brown and Gifford (1962) found a correlation between feed conversion and feed consumption of 0.709 and Bogart and England (1971) reported a value of 0.269. Both authors did not adjust feed used for maintenance. Koch et al. (1963) estimated a genetic correlation of 0.04 by adjusting for maintenance.

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Appendix

A quadratic regression has been used to describe weight changes during the 140 day performance test. The quadratic effect was highly significant except in 1970 where an almost linear gain has been observed. The method suggested below to adjust for maintenance takes in account this curvelinear growth.

A quadratic regression of weight on days-on-test has been fitted to each animals data points. The area under the curve divided by the length of the testing period in days is defined as average weight maintained (AWM).

$$AWM = \frac{1}{E-B} \int_{B}^{E} (b_0 + b_1x + b_2x^2) \, dx$$

$$= \frac{1}{E-B} \left(b_0E - b_0B + \frac{b_1E^2 - b_1B^2}{2} + \frac{b_2E^3 - b_2B^3}{3} \right)$$

Assuming $(b_2 = 0)$ then:

$$AWM = \frac{1}{E-B} \left(b_0E - b_0B + \frac{b_1E^2 - b_1B^2}{2} \right)$$

$$= b_0 + \left(\frac{E+B}{2} \right) b_1$$

$$= (mid\ weight)$$

Given ($B = 0$ days, $E = 140$ days and $b_2 \neq 0$) then:

$$AWM = b_0 + 70b_1 + \left(\frac{(140)^2}{3} \right) b_2$$

$$= (\text{mid weight}) + \left(\frac{(140)^2}{3} \right) b_2$$

b_2 negative $\Rightarrow$ $AWM < \text{mid weight}$

b_2 positive $\Rightarrow$ $AWM < \text{mid weight}$

SELECTION FOR FEED CONVERSION;
DIRECT AND CORRELATED RESPONSES AND GENETIC PARAMETERS

by

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Ing. Agr., Institute of Technology Zurich, 1974

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

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1976

Data from a selection experiment for feed conversion using a control population were analysed to calculate direct and correlated responses. Least squares estimates of line differences (selected vs. control) for the final year showed a cumulative selection response of 0.19 lb. less feed per lb. of gain. Associated with this response was a decrease in birth weight and weight at weaning. Average daily gain on test, average daily gain from weaning to yearling, and the relative growth rate during this period have increased. Selection for feed efficiency tended to lower height at yearling but yearling weight remained unchanged.

Loin eye area and backfat thickness were used as indicator of the stage of physiological maturity. No change in these traits were found due to selection.

A realized heritability of 0.44 has been calculated for feed conversion adjusted for maintenance. Heritabilities were also estimated by half sib correlations. The values estimated from 257 bull performance data were: birth weight, 0.42; 205 day weight, 0.31; 365 day weight, 0.41; average daily gain from birth to weaning, 0.37; average daily gain on 140 day postweaning test, 0.30; yearling height at shoulder, 0.56; total feed consumption on test, 0.40; feed conversion, 0.23; feed conversion adjusted for maintenance, 0.24; loin eye area, 0.11; and backfat thickness, 0.18. Heritabilities, calculated for bulls and heifers combined (n = 504) using the same method, were: Birth weight, 0.29; yearling height, 0.66; loin eye area, 0.15 and backfat thickness, 0.12.