# DIRECT AND CORRELATED RESPONSE TO FIVE GENERATIONS OF SELECTION FOR INCREASED POSTWEANING GROWTH UNDER AD LIBITUM OR A STANDARD LIMITED INTAKE IN THE PIG

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## NOMENCLATURE

| | |
|---|---|
| ACBF | carcass backfat averaged over three locations and adjusted to 104 kg |
| ADG | average daily gain |
| APBF | ultrasonically probed backfat averaged over three locations and adjusted to 104 kg |
| BW | pig birth weight |
| C | unselected control line |
| CUT | cutability defined as the proportion of closely trimmed wholesale cuts in the carcass |
| d | day |
| D42W | pig weight at 42 days of age |
| DG | overall daily gain from nine weeks of age through 100 kg |
| DG1 | growing phase daily gain from nine weeks of age through 54 kg |
| DG2 | finishing phase daily gain from 54 through 100 kg |
| D104 | age in days at 104 kg |
| D21W | pig weight at 21 days of age |
| F | line selected for increased gain from 36 through 104 kg under ad libitum intake |
| F' | line from previous project selected for increased gain from 9 weeks of age through 100 kg |
| FFG | fall farrowing group |
| FG | overall feed efficiency from nine weeks of age through 100 kg |

| | |
|---|---|
| FG1 | growing phase feed efficiency from nine weeks of age through 54 kg |
| FG2 | finishing phase feed efficiency from 54 through 100 kg FI overall daily feed intake from nine weeks of age through 100 kg |
| FI1 | growing phase daily feed intake from nine weeks of age through 54 kg |
| FI2 | finishing phase daily feed intake from 54 through 100 kg |
| g | gram |
| GFG | generation-farrowing group combination |
| kg | kilogram |
| L | line selected for increased gain from 36 through 104 kg under a standard limited intake |
| LDG | predicted daily lean gain from 9 weeks of age through 100 kg |
| LEA | tenth rib loin muscle area adjusted to 104 kg |
| LTFC | lean tissue feed conversion |
| LTGR | lean tissue growth rate |
| LWB | total litter weight at birth |
| LW42D | total litter weight at 42 days of age |
| LW21D | total litter weight at 21 days of age |
| m | meter |
| mm | millimeter |
| MOVE | subjective movement score given to a pig when removed from test |
| MSCORE | subjective carcass muscle score |
| NB | number of live pigs at birth in a litter |
| N42D | number of live pigs at 42 days in a litter |
| N21D | number of live pigs at 21 days in a litter |
| OFFWT | off-test weight for boars, 104 kg |

| | |
|---|---|
| ONWT | on-test weight for boars, 36 kg |
| PLEAN | estimated percent lean in the carcass |
| pST | porcine somatotropin |
| S | line from previous project selected for decreased gain from 9 weeks of age through 100 kg |
| SD | standard deviation |
| SFG | spring farrowing group |
| STRU | subjective strucuture score given to a pig when removed from test |
| TVOT | testicle volume at off-test weight |
| TV150 | testicle volume at 150 days of age |
| WCSD | weighted cumulative selection differential |
| wk | week |

# CHAPTER I

# INTRODUCTION

The overall goal of the swine industry should be the maximization of quality, saleable lean per unit of input. Advancement of this goal entails a large number of reproductive, growth and carcass traits, involving improvements in both genetic and non-genetic factors. The performance of a herd can only attain the level of that which is most limiting, either management or genetics. Management can result in rapid, but temporary progress. However, genetic improvement through selection is the only method to make permanent changes in a population.

Genetic improvements can be realized by two methods: selection and crossbreeding. Advancement within a line can only be accomplished by selection for the desired objective. The production of terminal offspring through the organized crossing of specialized lines takes advantage of heterosis or 'hybrid vigor' and allows breeds to compliment each other based on the strong points of each line or breed.

Specialized terminal or paternal lines should excel in postweaning traits such as growth, efficiency and carcass quality. In a terminal crossbreeding program the paternal line will contribute one-half of the genetic merit for postweaning traits, but does not contribute to reproductive traits since all offspring by terminal sires are sold. Therefore, the breeding objective for terminal lines should be increased lean growth and improved efficiency of lean growth.

Single-trait selection for growth and carcass traits has shown positive response in experimental lines of pigs. Selection for increased weight at a constant age (Krider et al., 1946; Kuhlers and Jungst, 1990; Kuhlers and Jungst, 1991ab) and for rapid postweaning gain (Rahnefeld, 1971; Fredeen and Mikami, 1986e; Woltmann et al., 1992) have been successful. Realized heritability estimates for gain or weight at a constant age ranged from .13 to .38. However, correlated response in one or more traits of importance is often unfavorable. The breeding objective is not improved as rapidly as possible with unfavorable response in some traits, therefore alternative selection methods for postweaning traits are of interest.

The traditional alternative to single-trait selection is an economic index that combines two or more traits into a single measurement. Estimates of heritabilities, phenotypic and genetic variances, phenotypic and genetic covariances and relative economic values for traits of interest are required for development of an economic index. The quality or realized response of the index is dependent on the accuracy of the estimates used.

Positive response to index selection has been reported in a number of studies. An index containing only gain and backfat resulted in progress for both traits (Vangen, 1974; Sather and Fredeen, 1977; Ollivier, 1980; Cleveland et al., 1982; McKay, 1990). Selection using this index generally resulted in improvements in lean growth rate and efficiency of lean growth. Selection on an index containing gain, backfat and feed conversion resulted in improvements in efficiency and backfat, but not growth rate (McPhee, 1981; Henderson et al., 1982). The improvements realized from selecting on this index were mainly the result of decreased appetite.

Fowler et al. (1976) proposed a more direct, biological model, as a method of selection for the postweaning breeding objective. The biological objectives or traits defined were lean tissue growth rate (LTGR) and lean tissue feed conversion (LTFC). Selection under an ad libitum nutritional environment allows intake to vary, thus genetic improvement in gain may be the result of correlated increases in appetite (Smith and Fowler, 1978). Selection for increased growth under an environment that removes intake variation would favor those animals that most rapidly and efficiently deposit lean. This is because about three units of lean tissue can be produced at the same energetic cost as one unit of fat tissue (Fowler et al., 1976). Webb and Curran (1986) discussed how goals related to selection for lean growth rate can be better achieved with an improved understanding of the relationship between feed intake and lean tissue growth under different feeding levels.

The realized heritability of gain in lines of mice that were selected under an environment in which intake variation was decreased or removed was similar to estimates in lines selected under ad libitum intake (McPhee et al., 1980; Hetzel and Nicholas, 1982; McPhee and Trappett, 1987). A line of mice selected for increased growth on ad libitum feeding grew faster, was more efficient (feed:gain), consumed more and partitioned more energy to fat than a line selected for increased growth on a restricted nutritional environment in progeny allowed ad libitum intake (McPhee and Trappett, 1987). However, the line selected under limited intake was more efficient at converting feed to lean tissue when fed ad libitum.

A single study has reported the results of selection under a restricted intake environment in pigs (McPhee et al., 1988). The selection criteria was increased ham weight after a 12 week period of restricted feeding. Select-line pigs were faster growing, more efficient, leaner and had increased ham weights when allowed either ad libitum or the restricted ration under which they were selected. However, this study lacked a line selected under ad libitum intake. Thus no direct comparison of selection under these intake environments has been made in the pig.

Two lines of pigs were established at the Oklahoma State Swine Breeding Laboratory to examine selection for increased growth under either ad libitum intake or a ration that removed daily intake variation. The terminal objective upon completion of seven generations of selection is to compare response in the breeding objectives of LTGR and LTFC in the lines under both feeding environments.

Responses in component traits of LTGR and LTFC (daily gain, feed intake, feed:gain and body composition) and reproductive and structural traits are hypothesized to differ depending on the intake level under which selection occurs. To test the above hypothesis the objectives of this study were to 1) quantify and compare responses in component traits of LTGR and LTFC to selection for gain under ad libitum or a standard daily intake and 2) quantify correlated responses in structural soundness and reproductive performance to selection for gain under ad libitum or a standard daily intake after five generations of selection.

# CHAPTER II

# REVIEW OF LITERATURE

Direct and correlated response to selection for postweaning traits in swine was reviewed by Woltmann (1989). Growth, efficiency, fat and indexes combining two or three of the above-mentioned traits are summarized in the present review of selection for postweaning traits whenever appropriate. Additionally, selection experiments in laboratory animals are reviewed to fill voids in the swine literature. All comparisons were to an unselected control unless otherwise specified.

## Selection for Growth in Swine

### Direct and Correlated Response

Selection for body weight or growth has been successful in a number of studies (Woltmann, 1989). The earliest report was by Krider et al. (1946), where lines of Hampshires were selected for high or low weight at 150 d of age. After nine generations of selection there was a 28.1 kg difference between the divergent lines at 180 d of age (Baird et al., 1952), with most of this difference established postweaning. The high-weight line gained more (.43 kg/d versus .14 kg/d), consumed more feed per day and was more efficient than the low-weight line when tested over a 72 day period (Baird et al., 1952).

A realized heritability of .13 was reported by Rahnefeld (1971) as the result of seven generations of selection for postweaning daily gain from 42 d through 89 kg. Rahnefeld and Garnett (1976) reported a realized heritability of .20 with the inclusion of four additional generations of selection. A correlated response in feed efficiency of .04 kg feed/kg gain after eight generations was much less than predicted (Rahnefeld, 1973). Additionally, no change in 42-d weight was found.

A series of papers reported direct and correlated response to nine generations of selection for: a) maximum daily gain from 56 d to test termination, b) decreased backfat at test termination and c) an index combining daily gain and backfat (Fredeen and Mikami, 1986abcde). Boars were tested in confinement and test was terminated at 91 kg, while gilts were tested on pasture and terminated from an average weight of 92 to 132 kg depending on the generation. Realized heritability in the growth and backfat lines was .20 and .28, respectively (Fredeen and Mikami, 1986e). Estimated genetic correlation between gain and fat was .07 for males and -.27 for the females (Fredeen and Mikami, 1986d). The difference in the correlations may have been due to sex, but was likely due to either environment, age or weight at termination of test.

The line selected for increased growth became less fat relative to controls (realized genetic correlation = -.51); however, the decreased fat line showed no improvement in gain relative to controls (realized genetic correlation = .02) (Fredeen and Mikami, 1986e). These two estimates of the genetic correlation, along with the within sex estimate (Fredeen and Mikami, 1986d) would suggest the genetic relationship between fat and gain is neutral to slightly favorable.

Response per selection measured in the index line was higher than the realized heritability in the single-trait gain line (Fredeen and Mikami, 1986e). The response per selection was .30 and .25 for the gain and fat lines, respectively. These are not estimates of realized heritability because the selection measured was indirect as a result of index selection.

Fredeen and Mikami (1986c) concluded based on the literature and their data that reproductive performance is enhanced by index selection for increased gain and decreased backfat. However, when single-trait selection is practiced on either trait individually reproduction is unaffected. In the index line, birth and weaning weight (42 d) were increased. No trend was seen for the two traits in the gain or fat line, even though there was a fairly large amount of indirect selection that occurred in each line (Fredeen and Mikami, 1986b). Meat quality was not adversely affected in any of the lines; however, total lean content was greater in select line carcasses (Fredeen and Mikami, 1986a). At generation nine the gain line had a predicted lean yield 1.4 % higher than the controls, while the fat and index lines were each about 5 % higher.

Selection for increased 70-d weight in Landrace (Kuhlers and Jungst, 1990), increased 200-d weight in Landrace (Kuhlers and Jungst, 1991b) and increased 200-d weight in a Duroc line (Kuhlers and Jungst, 1991a) was practiced for 5 or 6 generations. An average of three methods was used to estimate response to selection. Realized heritability for the Landrace 70-d weight line was .13 (Kuhlers and Jungst, 1990). The change in 70-d weight was the result of increased gain from 35 to 70 d. Co-heritabilities for weights at birth, 21 and 35 d of age were not different from zero, but for gain from 35 to 70 d the co-heritability was as large as the realized heritability estimate. This would suggest a genetic correlation of nearly one between 35 to 70 d gain and 70-d weight. Correlated response of growth or carcass traits beyond 70 d was not reported.

Realized heritabilities for 200-d weight were .18 in the Duroc line (Kuhlers and Jungst, 1991a) and .26 in the Landrace line (Kuhlers and Jungst, 1991b). Ultrasonic backfat thickness at 200 d was increased due to selection in both the Duroc and Landrace breeds. Much of this difference was due to larger weights in the select lines. When backfat was adjusted to common weight by the use of covariance analysis the regression of fat thickness on cumulative selection differential was non-significant. Carcass data taken from generation four of the

Duroc lines would suggest that the select line was fatter at a standard weight (Jungst and Kuhlers, 1987). Loin eye area did not differ, but select line carcasses had 9% more tenth rib fat depth at 104 kg and an estimated percent lean cuts 1.5 less than controls. Carcass data were not published for either Landrace line.

In addition to direct response in 200-d weight, increased weights at birth, 21, 35, 70 and 154 d were present at generation six in the Landrace line (Kuhlers and Jungst, 1991b). In the selected Duroc line, much of the response in 200-d weight was the result of growth from 154 to 200 days (Kuhlers and Jungst, 1991a). The regressions of response in weights and daily gains up to 154 d on cumulative selection differential were generally non-significant. Much like the Landrace line selected for increased 70-d weight, the co-heritability of growth during the period just prior to selection (154-200 d) was as large as the estimate of realized heritability. This would indicate selection for gain from 154 to 200 d in the Duroc breed would be equally effective in changing 200-d weight.

One additional study examined crosses between the Duroc and 70-d Landrace select and control lines mated in a 2 x 2 design (Bullock et al., 1991). There were no significant sire or dam line effects for daily gain from 70 to 165 d. Duroc sire effect differences for fat and percent lean were similar in magnitude to the line effect difference reported by Jungst and Kuhlers (1987); however, they were non-significant. In general, differences that resulted from selection were not passed on to their crossbred progeny.

Woltmann et al. (1992) reported the results of divergent selection for growth from 9 wk of age through 100 kg in a line selected for rapid daily gain (F) and one selected for slow daily gain (S). The ratios of divergent response to divergent cumulative selection differential were .38 and .37 for a spring and fall farrowing groups, respectively. Rapid line barrows from generations 2, 3 and 4 of the spring farrowing group consumed 17.5% more feed per day, gained 20.8% faster and had

15.8% more backfat than S barrows when fed ad libitum for a standard time period (Woltmann, 1989). When intake differences between F and S were removed, F gained 8.1 % faster and was 6.7 % more efficient. It was concluded that a large proportion of the line difference in growth rate under ad libitum intake was due to increased appetite in F, as compared to S. Much of the difference in food intake was partitioned as fat. Lean growth rate was 12.1 % higher in F under ad libitum intake, but efficiency of lean growth did not differ. Due to the lack of a control line it is impossible to determine whether these differences were due to selection for decreased gain, for increased gain or a combination of the two.

Jungst et al. (1981) selected for a decreased ratio of feed:gain. The realized heritability was .09; correlated decreases in backfat and daily food intake were non-significant. Only a 2.5% improvement in efficiency was observed after ten generations of selection (Bernard and Fahmy, 1970) and after six generations control and select lines did not differ in efficiency (Webb and King, 1983). Even though positive response has been reported and efficiency is of large economic importance, single-trait selection is probably not warranted. This is due to the relatively small amount of direct response, the cost involved in measurement of the trait and its favorable genetic correlation with gain. An alternative method of selection for efficiency (food:gain) would be feeding all pigs the same amount over a given time period. This would eliminate variation in intake, resulting in a perfect favorable correlation between growth and food:gain.

Summary of Selection for Growth

Realized heritability estimates for gain or weight at a constant age ranged from .13 to .38. In general, realized heritability estimates were less than those estimated by covariance and regression methods in non-selected populations. From a review of a number of studies, the average heritabilities for postweaning daily gain and age at a constant weight were .38 and .58, respectively (Hutchens and Hintz, 1981). Improvements in growth are accomplished through correlated responses in intake and efficiency. The relative importance of each is not clear and may be influenced a number of factors such as age selected, weight when selected and environment. McCarthy and Siegel (1983) in a review of selection for growth in poultry concluded that much of the intake differences between high and low growth lines of chickens were due to differences in feed consumption. In reviewing selection for growth in mice, Woltmann (1989) found that much of the literature suggested efficiency as a major correlated trait. However, at least one study found the differences in growth due to selection to be solely the result of intake differences.

In some studies, single-trait selection for growth either improved slightly or did not affect carcass composition (Fredeen and Mikami, 1986a, Kuhlers and Jungst, 1991ab). In others it was suggested that selection for increased growth resulted in decreased lean in the carcass (Jungst and Kuhlers, 1987; Woltmann, 1989). These disagreements in correlated response may be the result of selection for somewhat different traits and/or the endpoint at which the carcass was measured. The average genetic correlation between live backfat and postweaning gain was found to be zero (Hutchens and Hintz, 1981) and would suggest the genetic merit for carcass composition should not change when selecting for growth. However, single-trait selection for growth should not be recommended because of this apparent realized genetic correlation that is neutral to unfavorable with carcass composition.

## Index Selection for Postweaning Traits in Swine

### Biological Indexes

Bereskin and Steele (1986) discussed the need to measure and select for

LTGR and its efficiency, rather that gross weight gain and its efficiency. Genetic improvement of lean gain and efficiency is expected to follow one of two pathways under ad libitum feeding: a) increased rate of lean deposition or b) decreased rate of fat deposition through a reduction in voluntary food intake (Fowler et al., 1976). Lean growth and lean growth efficiency can be selected for using either a selection index that combines the component traits into a single measure or a more direct approach. The direct approach was defined by Fowler et al. (1976) as a "biological index". This is not an index, but rather single-trait selection, because the true trait of interest or the breeding objective is selected for in a more direct manner. The need for parameter estimates and economic values is eliminated.

Two biological indexes of economic importance are lean tissue growth rate (LTGR) and lean tissue feed conversion (LTFC) (Fowler et al., 1976). However, without practical and accurate methods to measure total body lean at the start and finish of test, the selection index will remain the method of choice for genetic improvement of LTGR and LTFC.

The components of LTGR are time and lean. Selection for this trait should result in increased lean growth and intake and no change in total fat (Fowler et al., 1976). The components of LTFC are food and lean. Selection for LTFC is expected to result in decreased fat and intake, but static lean growth. Selection under an ad libitum system using an index that favors lean and efficiency would tend to select those animals that voluntarily restrict their intake (Smith and Fowler, 1978). Under a time-scale feeding system all pigs are given the same allotment of feed based on time on test. This removes all intake variation, except that created by refusals, so selection would favor those animals that deposit lean more rapidly. Selection under this environment should result in a perfect correlation between LTGR and LTFC, since feed intake and days tested are constant for all animals.

Whittemore (1979) discussed the benefits of selecting animals with increased potential for LTGR. As pigs reach acceptable levels for backfat, the only way to improve the lean:fat ratio is to increase lean growth. He suggested that the upper level for lean growth had not been reached at that time. Even though this article was published 13 years ago, this statement is probably true in regards to all or most strains of pigs currently in the U.S. Recent studies using pST have shown substantial increases in lean growth with pST treatment (e.g., Etherton et al., 1986). This is an indication that an upper plateau for lean growth does not currently exist and improvements can be made as long as there is genetic variation exists.

Bichard et al. (1979) discussed a strategy to select for LTGR and/or LTFC. When selection is under a time-scale system, lean growth must be as close to optimum as possible to exert maximum pressure on LTGR. Intake needs to be near ad libitum, while eliminating most or all refusals. This means a good estimate of the mean and variance of intake in the population to be selected is important. In addition, a pig should not be limit fed during early stages of growth (<35 kg), since it may not consume enough food to support maximum lean growth during this period.

A study was undertaken in which boars were offered ad libitum or 96% of ad libitum intake over a constant time period (Bichard et al., 1979). The boars on the limited level consumed only 84% of predicted ad libitum. Levels very close to ad libitum intake should not be used to eliminate intake variation. It was suggested that pigs be scale fed at 80 to 90% of ad libitum after reaching 40 kg. Feeding at this level would remove most refusals and allow for near maximum lean growth.

Direct and Correlated Response

As compared to single-trait selection for postweaning traits, a large number of studies have reported the results of selection using an index that included two or three traits . A selection index combining growth and carcass traits is expected to have the same objectives as a biological index (Fowler et al., 1976). Without accurate methods to measure composition at the beginning and end of the testing period, the selection index will be the method of choice over the more direct biological index method.

Response to selection on an index of gain and backfat was reported in a number of studies (Vangen, 1974; Sather and Fredeen, 1978; Ollivier, 1980; Cleveland et al., 1982; McKay, 1990).

Vangen (1974) selected on divergent phenotypic indexes: an upward index of increased gain and decreased backfat and a downward index of decreased gain and increased backfat. A phenotypic index that was intended to weight the traits equally based on their phenotypic standard deviations was used. Efficiency was improved and growth rate increased in the upward line. As expected, response was unfavorable for both traits in the low line. Appetite was initially unaffected by selection for decreased fat and increased gain (Vangen, 1977), but daily intake was later reported to have significantly increased by .006 kg/generation (Vangen, 1980). These lines were selected under a "semi-ad libitum" feeding regime, in which pigs were fed twice daily to appetite.

Vangen (1979) reported per generation responses of -.7 mm for backfat and 6.7 g for daily gain. The realized response in the high line was .55, .61 and .41 for the index, backfat and gain, respectively. Improvements in LTGR and LTFC appeared to have resulted from selection for increased gain and decreased backfat (Vangen, 1980), but neither of these traits were measured directly.

A similar phenotypic index of gain and backfat resulted in improvements in both index traits (Sather and Fredeen, 1978). Response per selection in the index line was .30 and .25 for gain and backfat, respectively (Fredeen and Mikami, 1986e). Total intake from 56 d to 90 kg was decreased, thus the improvement in growth rate was the result of improved efficiency (Sather and Fredeen, 1978). However, there were no line differences when intake was expressed on a daily basis. Additionally, correlated responses in the index line were reported for increased birth and weaning weight (Fredeen and Mikami, 1986c) and percent carcass lean (Fredeen and Mikami, 1986a).

A third study selected for a phenotypic index of gain and backfat (McKay, 1990). Even though both traits were standardized by their estimated phenotypic standard deviations, very little selection pressure was placed on daily gain. Response per generation for backfat was -.70 and -.35 mm for a Yorkshire and Hampshire line, respectively. Response per generation for daily gain was not different from zero for either breed.

Cleveland et al. (1982) selected for the same two traits in an economic index. This index placed more emphasis on daily gain in standard deviation units than backfat. In a comparison of this index to the one reported by Vangen (1979), relatively more emphasis was placed on daily gain. Backfat was decreased by 5.4% and daily gain increased by 12.5% after five generations of selection. The realized heritability of the index was .19; however, only 41 and 38% of expected response was realized for gain and backfat, respectively. Barrows from the index and control lines were individually fed starting at 25 kg for a constant time period. Pigs from each line were tested on one of three rations: ad libitum, 91% of predicted ad libitum or 82% of predicted ad libitum (Cleveland et al., 1983a). Lean gain was greater in the index line by 70 g/d at the two highest feeding levels. However, at the 82% restriction level the line difference was only 17 g/d. Lean growth was depressed to a greater extent in the index line when restricted to the 82% level (21 vs. 11%), as compared to ad libitum. This may have been due to an inadequate level of protein to support the higher amount of lean growth potential.

The index line was more efficient both on a live weight and lean weight basis

(Cleveland et al., 1983b). The 91% level of restriction was the most efficient intake level for depositing lean. Barrows at this level were 5% more efficient, but gained 10% more slowly. The regressions of correlated response on cumulative selection differential in litter size and pig weight were not significant (Cleveland et al., 1988).

Lean tissue feed conversion was the breeding objective of an index that included increased growth rate, improved feed conversion ratio (feed/gain) and decreased backfat (McPhee, 1981). Pigs were tested from 45 to 80 kg under a semi-ad libitum feeding regime, in which pigs were allowed to consume ad libitum for 20 minutes. Response was evaluated in two feeding trials when selection was terminated after 4.3 generations of selection. The select line gained faster when fed a limited ration, but the control line gained faster when fed ad libitum. The decreased growth in the select line was due to a 6.4% lower voluntary food intake; however, the select line was more efficient and had about 12% less backfat. Selection using this index improved LTFC, the biological trait selected for, by 7.5 and 5.8% under ad libitum and restricted feeding level, respectively. Lean growth rate was improved by 5% under limited intake, but under an ad libitum environment this difference was only 1.5%. Selection had its effect by decreasing intake, and to a lesser extent by increasing lean growth rate.

Long-term selection using an economic index containing the same three traits was reported in a second study (Henderson et al., 1982). Feed conversion data were collected from pens of 2 or 3 full-sibs allowed ad libitum intake from 27 to 87 kg. Ellis et al. (1988) reported a realized heritability for the index of .26 through 11 generations of selection. A total increase of 45 index points resulted in realized improvements of 20 and 9% for backfat and feed conversion, respectively. No improvements in daily gain were accomplished, even though a large realized cumulative selection differential was achieved. This index placed less emphasis on daily gain, as compared to an index containing the same traits currently used at

U.S. central boar test stations (NSIF, 1987).

Improvements in efficiency and backfat were mainly the result of decreased intake (Smith et al., 1991), as was predicted by Fowler et al. (1976). Select-line boars consumed .25 kg less food per day from 30 to 90 kg. Annual reductions were -.012 and -.017 kg/d for the boars and gilts, respectively. The intake difference of .25 kg was uniform over the weight range examined; however, at lower weights the reduction was proportionately higher. In these young males the daily intake was not sufficient to promote maximum lean growth.

A number of earlier studies reported on these lines at generation 10 of selection. Line differences for growth and fat were already established at on-test weight (Henderson et al., 1982). At 27 kg select boars were nine d older and had a lower proportion of dissected carcass fat. Body fat was not relocated from subcutaneous to other fat sites as the result of selection; however, some redistribution of subcutaneous fat appears to have occurred (Wood et al., 1983). There were no differences detected for bone and lean weight distribution.

Companion papers reported on feeding males from the select and control lines at either ad libitum (Ellis et al., 1983) or at the same level for a fixed time (Henderson et al., 1983). In both trials boars were started on test at 27 kg and fed for 84 d. Select boars gained faster and were thus more efficient when intake differences were removed. Carcass dissection revealed that differences remained, even though intake differences were removed. The select line contained 7% more lean, 6% less fat and was 9% more efficient in converting food to lean. These differences were greater under the ad libitum feeding environment. The select line contained 9% more lean, 13% less fat and was 18% more efficient in converting food to lean. Control boar intakes were 4% higher over the entire 84 day period, but most of this difference was the result of increases during the first 42 days. This differed from Smith et al. (1991), as discussed earlier, where a constant difference in voluntary intake of .25 kg/day from 30 to 90 kg was reported.

Leymaster et al. (1979) used a more biological approach in selecting for lean tissue growth and lean tissue efficiency. Lines of Yorkshires were selected for percent lean cuts at a constant weight or total carcass lean at a constant age. Direct selection for total lean cuts resulted in an increase of .50 kg/generation and a correlated response in percent lean of .23%/generation. Selection for percent lean resulted in a direct response of .38%/generation resulted and a non-significant decrease in total lean cuts. Realized heritabilities for percent lean cuts and total lean cuts were .32 and .17, respectively. The estimated genetic correlation between percent lean and total lean cuts was .22 ± .18.

Correlated responses for backfat of .03 and .10 mm/generation were reported for the total lean and percent lean lines, respectively (DeNise et al., 1983). Correlated responses in overall growth or lean growth rate were not reported. Selection did not effect carcass quality, conception rate or farrowing rates. However, in both select lines litter size was adversely affected. Litter size was smaller at birth, 7 and 21 days. For second parity sows litter size at 21 days was about 2 pigs less.

Summary of Index Selection

Positive response in index points was reported in five separate studies for a selection index that included gain and backfat. Lean growth rate and the efficiency of lean growth improved as the result of index selection for these two traits. Two studies reported favorable response on an index of gain, efficiency and backfat. In both studies intake decreased and gain remained constant. The net result was an improvement in lean growth efficiency, but little or no change in lean gain.

The amount of response realized in each index and the component traits varied between studies. The expected and realized response per trait is dependent on the relative weight given to each trait. This will depend on the type of index, either phenotypic or economic. If an economic index is used the weighting of each trait will be affected by the relative economic values placed on each trait. In addition, an index is dependent on the parameter estimates used, including heritabilities and the genetic and phenotypic covariances.

An alternative to index selection is the biological index. The objective is selected for more directly, rather than by an index of component traits. This method eliminates the need for the parameter estimates and economic values that are required to derive an economic index, but has certain limitations. To estimate lean growth the initial and final lean content of the pig must be estimated. Without accurate methods to estimated lean content, pigs will not be ranked appropriately. Also, the biological model does not allow for the inclusion of many economically important traits, such as reproduction.

## Selection for Growth Under Limited Intake

### Direct and Correlated Response in Mice

Few studies in swine have reported response to selection for growth under limited intake, thus the literature pertaining to mice will be summarized.

Early experiments that included lines selected for growth under limited intake were designed to study genotype by environment interactions (Dalton, 1967; Falconer, 1960). Falconer (1952) expressed the interaction between the two nutritional environments as a genetic correlation between separate traits. The only justification for selecting under the environment opposite that in which the animal is expected to perform would be an increased heritability in the environment the parents are selected under. The smaller the genetic correlation between the two traits or environments, the larger the heritability must be to justify selection under the opposite environment.

More recent experiments that have included lines selected under limited intake have been designed to answer questions related to the partitioning of metabolizable energy. McPhee et al. (1980) hypothesized "when animals are fed the same amount over the same period, selection for the fastest growers would result in partitioning of metabolizable energy toward more protein and less fat". This should result in selecting for animals that are improved in both lean growth rate and lean growth efficiency, as discussed by Fowler et al. (1976).

McPhee et al. (1980) selected for increased growth rate in mice from 5 to 9 wk of age under an intake level that was 83% of estimated ad libitum. The realized heritability of this trait was estimated to be .36 and .19 in replicated selection lines. No line selected for increased growth under ad libitum intake was included. Even though selection response was positive, the hypothesized changes in carcass composition did not occur. Select and control line mice from the sixth generation of selection were fed either ad libitum or limited intake levels. The select line had more total fat, a higher percent fat and lower percent protein when fed either ad libitum or the limited intake level. It should be noted that selection did not occur until after the period of rapid protein deposition for mice, so selection may not have been for the desired changes in carcass composition. It was concluded that a reduction in the maintenance requirements may have accounted for the line differences in growth rate. The authors suggested that gross weight gain may be too crude a measurement and that direct measurement of composition may increase rate of response in lean composition.

The same laboratory conducted a similar selection experiment that corrected many of the problems of the earlier study (McPhee and Trappett, 1987). Lines of mice were selected for increased 3 to 6 wk growth under either an unrestricted nutritional environment (F) or one that was restricted to 80% of predicted ad libitum (L). Realized heritabilities, estimated by a ratio of response to the cumulative selection differential, were .38 and .33 for F and L, respectively. The control line was randomly selected under ad libitum intake. Also, the cumulative selection differential was 50% higher in F (.63 vs. .42 g/d), than L. This was an indication that the phenotypic variation of growth was decreased when all mice were fed the same amount of food.

Mice representing seven generations of selection were allowed either ad libitum intake or 80% of predicted ad libitum in a 2 x 2 factorial arrangement with selection line. From this arrangement the realized genetic correlation was estimated to be .54. Each line performed better under the diet which they were selected. Ad libitum intake increased in F and decreased in L and in gross efficiency responded favorably in both lines. Compared to the controls, the select lines contained more carcass protein. However, the ratio of protein to fat was highest in L under both feeding regimes. The authors concluded that if the breeding objective is efficiency of lean growth, then restricted feeding is the best nutritional environment for selection.

The same selection criteria as above were used by Hetzel and Nicholas (1982), but an ad libitum and a restricted control line were maintained rather than a single ad libitum line. Realized heritability was .29 and .19 for the F and L lines, respectively. The phenotypic variation of weight gain was 2.5 times larger in the F line. As discussed earlier, the selection differential reported by McPhee and Trappett (1987) also suggested a decrease in daily gain variation when selecting under a limited intake.

As in the previous studies, a 'switch-back' design was used to evaluate each of the lines under both feeding environments (Hetzel and Nicholas, 1986). The estimated genetic correlation between growth under the two environments was .28.

When all lines were fed at the same intake level, L gained the fastest and was thus the most efficient. Under both feeding environments F had the highest rate of fat deposition and L the lowest. The use of restricted feeding allowed the exploitation of heritable variation in the partitioning of energy for growth.

Direct and Correlated Response in Swine

Only two studies have been designed to compare response to selection under different levels of intake in the pig (Fowler and Ensminger, 1960; McPhee et al., 1988). The early study (Fowler and Ensminger, 1960) was designed to explore genotype by environment interaction. High and low (intake 70% of high) nutrition lines were selected on an index of gain and litter size. No control line was maintained. Pigs representing generations 7, 8 and 9 were studied in a 'switch-back' design. The estimated genetic correlation of growth under the two nutritional environments was .70. When both lines were allowed ad libitum intake, the low line grew more rapidly in two of the three generations and equal to the high line in the third. This was because the low pigs were more efficient. When both were fed the restricted ration performance of the low line was superior to the high in each generation.

It was suggested that superiority in growth of the high line was due to their potential intake capacity. For this reason they were unable to compete with the low line when both were fed a restricted level of intake. The authors also suggested that the superiority in feed efficiency of the low line pigs may have been due to a lowered metabolic rate and/or repartitioning of growth from fat to lean.

Selection for lean growth, as measured by weight of ham lean, was practiced under a restricted level of intake for 4.5 generations (McPhee et al., 1988). Pigs were tested for 12 wk starting at a weight of 25 kg. Pigs were limited to the same amount of food daily, such that all pigs received the same amount of food over the 12 week period. The weight of ham lean was predicted from growth rate and ultrasonic fat depth. A line selected for increased ham under ad libitum intake was not included in this study.

Response was measured under a feeding regime of either ad libitum or the restricted ration under which they were selected. The select line grew faster, was leaner, had a higher weight of ham lean and was had a lower feed:gain than the control when fed at either intake level. These differences were larger under ad libitum intake, except for fat. Ad libitum intake was higher in the select line.

A high genetic correlation was implied between ad libitum and the restricted feeding levels by the similarity in realized response. The authors suggested that selection for lean under ad libitum intake, if practiced, may have been slower. This is based on the above-mentioned high genetic correlation, the higher heritability for ham weight under limited intake (.43 vs. .28) and a small, favorable correlation between growth and fat under limited intake. The genetic correlation between fat and growth under ad libitum intake was estimated to be small, but unfavorable.

Line differences were observed to be subject to seasonal variation. Since the generations were not distinct, testing of pigs within a generation occurred throughout the year. Differences between lines were greatest during the cooler months, with the most marked differences in backfat. No explanation for these seasonal affects were discussed.

Two additional studies relating to these lines were reported in the literature (McPhee et al., 1991a; McPhee et al., 1991b). The select line responded to higher levels of lysine (20 vs. 17 g/d) through decreased fat and increased gain when fed to a restricted level of intake (McPhee et al, 1991b). This response was at a "medium" energy density diet; there was no additional response at a "high" energy level.

McPhee et al. (1991a) found the effects of selection and porcine somatotropin (pST) to be additive. The select line examined were described by McPhee et al. (1988). Selection increased growth rate 22%, improved efficiency 14% and decreased backfat by 14%. Treatment with pST produced similar improvements of 17, 20 and 15% across lines for the same three traits, respectively. Selection had no adverse effects, but pST had a slight undesirable effect on lean quality. Selection worked through a combination of increased appetite and repartitioning of fat to protein, but pST worked solely through repartitioning.

A major problem associated with selection under a environment different from that in which the offspring will be expected to perform is the possibility of a selection regime x production system environment interaction (Webb and Curran, 1986). Selection under a limited environment does not account for genetic intake differences, and thus will change the ranking of boars (Kanis, 1990a). The easiest way to avoid this interaction is allow pigs ad libitum access under both test and commercial conditions. However, a better understanding of the reasons for these interactions is needed. A long-term selection project is currently underway in Britain that is designed to better understand the genetic relationships between lean tissue growth rate (LTGR), lean tissue feed conversion (LTFC) and feed intake, as described by Webb and Curran (1986). Divergent lines are being selected under four criteria: a) LTFC allowed ad libitum intake; b) LTGR allowed ad libitum intake; c) LTGR at a restricted intake level; d) voluntary feed intake. In addition, ad libitum and restricted intake control lines will be maintained.

Lines of mice were selected under ad libitum intake for either increased appetite, decreased fat proportion or increased lean mass (Hastings and Hill, 1989). Direct response occurred in each line; however, the only line that had a desirable change in carcass composition was the line selected for fat proportion. In the other two lines fat changed at a rate that was proportionate to lean.

Summary of Selection for Growth Under Limited Intake

The earliest reported studies involving selection under a limited level of intake were designed to examine genotype x environment interactions. More recent studies have removed the variation in daily intake to attempt to exploit heritable variation in the partitioning of metabolizable energy.

In mice, realized heritability estimates for growth under restricted intake were in the range of those reported for growth under ad libitum intake. Selection under limited intake appears to be a successful method of selecting for lean tissue efficiency.

In swine, single trait selection for growth under limited intake has not been reported. Favorable response was reported when a line was selected for increased ham weight under limited intake. The select line was leaner, more efficient and grew faster when fed either ad libitum or the diet under which they were selected. However, a contemporary line selected under ad libitum intake was not developed, thus a direct comparison of the two feeding environments is not available.

## The Role of Intake

The role of appetite or voluntary food intake is undoubtedly important in the overall genetic improvement of pigs. A number of authors has discussed the importance of appetite in regard to further genetic improvement of the pig (Fowler, 1986; Kreiter and Kalm, 1986; Webb and Curran, 1986; Vangen and Kolstad, 1986; Brandt, 1987; Kanis, 1990b). The degree to which appetite is correlated with economically important traits such as gain, backfat and efficiency will determine how the genetic potential for intake is affected. This is because intake is not directly selected for in indexes commonly used by the United States or European swine industries.

It should be noted that all of these papers are by European authors. Much more emphasis has been placed on efficiency of lean deposition and percent lean in Europe, thus reduced genetic potential for appetite is a larger problem than in the United States. However, these ideas are very applicable to the long-term improvement of pigs in the United States.

Index selection experiments that have included gain, backfat and/or efficiency are one way to study correlated intake response due to selection. Selection experiments with the objective of improving the efficiency of lean tissue growth have used an index of increased growth and decreased fat under ad libitum (Sather and Fredeen, 1978; McPhee, 1981; Cleveland et al., 1983) or semi ad libitum intake (Vangen, 1979) or an index of gain, backfat and feed conversion efficiency under ad libitum (Ellis et al., 1983) or semi ad libitum intake (McPhee, 1981). Feed intake of selected lines has fallen below the levels of controls in all but one of the studies (Vangen , 1979), in which intake was unchanged relative to the control line. Pigs were selected under semi ad libitum intake in this study, thus the variation in intake of the selected animals was reduced. Cleveland et al. (1983) did not report feed intake. In a comparison of the expectations for indexes emphasizing efficiency of lean growth, feed intake and gain are expected to decrease when testing is under ad libitum intake and increase when tested under limited intake (McPhee et al., 1979). An alternative to prevent deterioration of intake when testing is under an ad libitum environment, is the use of a selection index that restricts change in intake.

The reduction in intake reported by most studies is largely due to the antagonistic genetic correlation between ad libitum intake and backfat. McPhee et al. (1979) and Brandt (1987) reported correlations of .59 and .49, respectively. Vangen (1980) found this correlation to be only slightly unfavorable under semi-ad libitum intake, which may explain why intake was unaffected by index selection in one study (Vangen, 1979).

A review of heritability estimates for intake indicated a range of estimates from .12 to .59 (Standal and Vangen, 1985). Heritability was higher when estimated under ad libitum intake, as compared to semi ad libitum. McPhee et al. (1979) reported an average heritability of .38 for the studies that were reviewed, pointing out that the heritability of feed intake is affected by feeding level, diet, temperature and other environmental conditions. More recently, Brandt (1987) reported an estimate of .50.

The genetic correlation between gain and intake is high, thus decreases in intake must be avoided to prevent further deterioration of growth (Brandt, 1987). Reviews of the literature (Wyllie et al., 1979; Standal and Vangen, 1985) found the genetic correlation between gain and ad libitum intake to be about .90. Under restricted or semi-ad libitum intake this correlation is much lower (about .50). In fact, if intake variation is totally eliminated this correlation will by definition become zero. Even though the relationship between ad libitum intake and gross gain is very strong, Kreiter and Kalm (1986) reported a moderately favorable genetic correlation of .40 for lean growth and intake. Also, an unfavorable correlation between intake and backfat of .50 was reported.

Webb (1986) stated that once optimum fat levels are reached then selection emphasis should shift from efficiency of lean growth toward rate of lean growth. The author suggested selection methods that increase appetite and protein synthesis will result in greater overall improvement over a number of generations. A better understanding of the genetic relationship between voluntary feed intake and lean tissue growth under different feeding regimes is needed to better accomplish selection goals related to lean growth (Webb and Curran, 1986). A number of methods have been proposed to emphasis long term improvements in lean growth and are discussed below.

The simplest way to emphasize intake is to place more economic emphasis on growth when deriving a selection index (Kreiter and Kalm, 1986). Two other potential improvement methods are selection using an index that restricts changes in intake or direct selection for lean growth rate. Brandt (1987) discussed the same three alternatives. The author stated two main problems with the biological approach. First, lean growth is hard to measure accurately because of the inability to accurately estimate lean at the beginning and end of test. Second, traits such as meat quality and female performance cannot be incorporated into the model. He concluded that restricting changes in the genetic potential for intake within an index is the best way to prevent further declines for that trait.

## Prediction of Carcass Lean

Estimation of lean composition is important in the carcass, as well as the live animal. As the technology to evaluate carcass composition in the live animal becomes more accurate, total lean content of the live animal can be evaluated with increased accuracy. This will allow for a more biological approach (Fowler et al., 1976) to selection for postweaning traits. Most of the published research to predict lean is the result of measurements on the whole carcass followed by complete tissue separation of the carcass into lean, fat and bone. To allow for more accurate prediction of and selection for lean growth specific methods using the Real-Time technology needs to be developed. Genetic parameter estimates for such things as Real-Time muscle area and lean growth are not readily available in the literature.

Industry standardized prediction equations for lean composition are available for carcass ranking and are updated periodically (Fahey et al., 1977; Grisdale et al., 1984; Orcutt et al., 1990). In all three studies the best predictor of carcass composition was tenth rib fat depth. In addition, loin muscle area and carcass or live weight are used to predict total lean.

The previous equations adapted from Grisdale et al. (1984) overestimated carcass lean and were giving the current United States pork industry a false security (Orcutt et al., 1990). The authors suggested the equations need to be updated frequently to keep up with the changing industry. Powell et al. (1983) found that the equations in place at that time (Fahey et al., 1977) overestimated lean in low cutabiltity carcass, but were effective at ranking the carcasses on percent lean. Another study of the same equations found that the estimation methods based on intact carcass scores were inaccurate (Edwards et al., 1981). However, they found the equations that used tenth rib fat depth and loin muscle area were appropriate over a wide range of fat thicknesses.

Measures of fat depth at the tenth rib or fat thickness at the last rib were the best single predictors of carcass lean and explained from 50 to 70 % of the variation in total lean (Diestre and Kempster, 1985; Kanis et al., 1986; Kempster and Evans, 1979; Wood and Robinson, 1989). Kempster and Evans (1979) found a single ultrasonic measurement in 61, 91 and 118 kg pigs explained 62 % of the variation in cold carcass lean content over all three weight ranges. Additional fat measurements only slightly improved the prediction equations. A similar percentage of total lean (50 to 62%) was explained by a combination of live weight and any two ultrasound fat thicknesses (Kanis et al., 1986).

There is some evidence that breed or genetic type may affect prediction. Using a pooled equation, percent lean was overestimated by .5% in Large Whites, but was underestimated by 1.8% in Pietrains (Wood and Robinson, 1989). Carr et al. (1978) found that growth of backfat was linear in Hampshires from 45 to 136 kg. Growth in loin muscle area was quadratic as the result of a decreased rate of loin muscle deposition as pigs reached heavier weights. In Yorkshires, growth in loin muscle area was linear over the weight range. These differing growth patterns would affect prediction of and ranking on lean, especially in those equations that adjust lean to a constant weight.

Prediction of lean in a genotype can be predicted from the dissected ham (Evans and Kempster, 1979). If full dissection is cost prohibitive, dissection of the wholesale ham is the most accurate and is relatively low in cost. The same authors evaluated lean prediction using single wholesale cuts when pigs were fed under different levels of feed intake. The shoulder area was the most stable across different restriction levels. However, dissection of the loin area should be avoided because of it's inability to predict lean content across levels of dietary restriction.

To allow for the estimation of lean growth over a specified weight range, an accurate estimate of carcass lean at on-test weight is required. Prince et al. (1981) suggested a four variable equation to predict total body lean in 25 to 45 kg pigs: including body weight, average of three ultrasonic backfat measurements, body length and ultrasonic loin depth. This equation had an $R^2$ of .89. A simpler equation was suggested for 15 to 50 kg pigs that included only body weight (Brannaman et al., 1984). A nearly identical equation was used by Woltmann et al. (1992) to predict the composition of 30 to 50 kg pigs. The latter equations would suggest that lean growth is proportional to total growth from 15 to 50 kg.

## Summary

Direct response to selection for postweaning growth and/or carcass traits in swine was reported to be positive for all single-trait and index studies reviewed. Unfavorable correlated responses are often associated with single-trait selection, thus the overall postweaning objective of either increased lean growth or improved lean growth efficiency is not optimized. Selection solely for growth or gain has resulted in small improvement in gross efficiency, neutral to slightly unfavorable changes in fat thickness and percent carcass lean and increases in intake. The degree to which fat increases depends on the extent to which the increased intake is above the pigs need for maintenance and lean growth.

Index selection should result in maximum progress toward the overall breeding objective. Response to selection on an index of gain and fat was favorable for both traits. In addition, lean growth and lean efficiency were improved when selecting on this index. An index of gain, fat and feed conversion improves the efficiency of lean growth. The improvement in this index is realized through correlated decreases in appetite. This change in intake results in improved feed conversion and decreased fat, but no change in gain.

Selection for postweaning traits on a limited ration removes much or all of the intake variation. When intake is similar for all pigs, those that gain the most rapidly partition more of their metabolizable energy toward lean growth. Mice studies suggest that if lean efficiency is the breeding objective, removal of intake variation will increase response more rapidly than selection under ad libitum intake. Growth improvements in a line of pigs selected under ad libitum intake appeared to be the result of increased appetite, but progress in a line selected for gain under a limited intake level was the result of both reduced maintenance and the repartitioning of growth from fat to lean. Positive response in ham weight was realized when selection was under a restricted intake. A contemporary line was not selected under ad libitum intake, thus a direct comparison of selection under the two feeding levels was not available. However, it was suggested that direct response was more rapid under restricted feeding than it would have been under ad libitum feeding.

## CHAPTER III

## DIRECT AND CORRELATED RESPONSE TO FIVE GENERATIONS OF SELECTION FOR INCREASED POSTWEANING GROWTH UNDER AD LIBITUM OR A STANDARD LIMITED INTAKE IN THE PIG

### Abstract

Lines of pigs were established to compare component traits of lean tissue growth rate and lean tissue feed conversion (gain, intake, feed:gain and body composition) Selection was practiced for increased postweaning daily gain (DG) from 36 to 104 kg under either ad libitum (F) or a standard limited (L) intake. An unselected control line (C) allowed ad libitum access to feed was also maintained. Selection was on males only for five generations in a spring (SFG) and a fall (FFG) farrowing group. Response was measured on barrows and gilts allowed ad libitum access to feed from 9 wk of age through 100 kg. Barrows and gilts were penned together by line and pen feed intake was measured. Ultrasonic backfat (APBF) measurements were taken on all pigs at test termination. In generations 3, 4 and 5 one barrow per litter was slaughtered and carcass data collected. Additional information collected only in generation five included movement and front-end soundness scores on barrows and gilts and testicle volume in boars. Response per generation and per weighted cumulative selection differential (WCSD) were estimated. Standardized WCSD were 3.4, 3.6, 2.8 and 3.1 for F-FFG, F-SFG, L-FFG and L-SFG, respectively. Realized responses per generation averaged over farrowing groups were .13±.06 and -.04±.18 for F and L, respectively. Component trait regressions were significant (P<.05) for increased daily intake in F and decreased backfat and improved feed:gain in L. In generation five, F was greater (P<.05) for DG and daily intake; however, L had advantages (P<.05) in decreased backfat and improved feed:gain. Lean growth rate, estimated from barrow carcass data, was higher in F than in L (P<.05). These data indicate that response in the component traits of lean tissue growth rate and lean tissue feed conversion are dependent on the allowed intake environment under which selection occurs. In F, favorable response in DG was mainly the result of increased intake. In L, improvement in feed:gain was the result of decreased intake in relation to gain. Selection under an environment that removed variation in daily intake exploited heritable variation differently than selection under an ad libitum nutritional environment.

## Introduction

Single-trait selection for growth and carcass traits has shown positive response in experimental lines of pigs. Selection for increased weight at a constant age (Krider et al., 1946; Kuhlers and Jungst, 1990; Kuhlers and Jungst, 1991ab) and for rapid postweaning gain (Rahnefeld, 1971; Fredeen and Mikami, 1986e; Woltmann et al., 1992) has been successful. Realized heritability estimates for gain or weight at a constant age ranged from .13 to .38.

Positive response to index selection has been reported in a number of studies. An index containing only gain and backfat resulted in progress for both traits (Vangen, 1974; Sather and Fredeen, 1977; Ollivier, 1980; Cleveland et al., 1982; McKay, 1990). Selection using this index generally resulted in improvements in lean growth rate and efficiency of lean growth. Selection on an index containing gain, backfat and feed conversion resulted in improvements in efficiency and backfat, but not growth rate (McPhee, 1981; Henderson et al., 1982). The improvements realized from selecting on this index were mainly the result of decreased appetite.

Fowler et al. (1976) proposed a more direct, biological model, as a method of selection for the postweaning breeding objective. The biological objectives or traits defined were lean tissue growth rate (LTGR) and lean tissue feed conversion (LTFC). Selection under an ad libitum nutritional environment allows intake to vary, thus genetic improvement in gain may be the result of correlated increases in appetite (Smith and Fowler, 1978). Selection for increased growth under an environment that removes intake variation would favor those animals that most rapidly and efficiently deposit lean. This is because about three units of lean tissue can be produced at the same energetic cost as one unit of fat tissue (see Fowler et al., 1976). Webb and Curran (1986) discussed how goals related to selection for lean growth rate can be better achieved with an improved understanding of the relationship between feed intake and lean tissue growth under different feeding levels.

The realized heritability of gain in lines of mice that were selected under an environment in which intake variation was decreased or removed was similar to estimates in lines selected under ad libitum intake (McPhee et al., 1980; Hetzel and Nicholas, 1982; McPhee and Trappett, 1987). A line of mice selected for increased growth on ad libitum feed grew faster, was more efficient, consumed more and partitioned more energy to fat than a line selected for increased growth on a restricted nutritional environment in progeny allowed ad libitum intake (McPhee and Trappett, 1987). However, when limited to the same intake level the line selected under restricted feeding grew faster and was more efficient

A single study has reported the results of selection under a restricted intake environment in pigs (McPhee et al., 1988). A line was established by selecting for increased ham weight under restricted feeding. Select-line pigs were faster growing, more efficient, leaner and had increased ham weights when allowed either ad libitum or the restricted ration under which they were selected. However, this study lacked a line selected under ad libitum intake. Thus no direct comparison of selection under these intake environments has been made in the pig.

Two lines of pigs were established at the Oklahoma State Swine Breeding Laboratory to examine selection for increased growth under either ad libitum intake or a ration that removed daily intake variation. The terminal objective upon completion of seven generations of selection is to compare response in the breeding objectives of LTGR and LTFC in the lines under both feeding environments.

Responses in component traits of LTGR and LTFC (daily gain, feed intake, feed intake and body composition) and reproductive and structural traits are hypothesized to differ depending on the intake level under which selection occurs. To test the above hypothesis the objectives of this study were to 1) quantify and compare responses in component traits of LTGR and LTFC to selection for gain under ad libitum or a standard daily intake and 2) quantify correlated responses in structural soundness and reproductive performance to selection for gain under ad libitum or a standard daily intake after five generations of selection.

## Materials and Methods

### Initiation of lines

The base generation was established at the Southwest Forage and Livestock Research Station near El Reno from a line of pigs that was previously selected for rapid growth from 9 wk of age through 100 kg (F'). Development of this line was described by Woltmann (1989) in a comparison of F' and a line selected for slow postweaning growth (S) over the same period. The selection lines were replicated in spring and fall farrowing groups. The spring group (SFG) farrowed from mid-March through April and the fall group (FFG) farrowed from mid-September through October. Establishment of a base generation was accomplished by cross-classifying males with farrowing groups. Males born in the spring of 1984 sired the pigs born in the fall of 1985. Likewise, males born in the fall of 1984 were used to sire the pigs born in the spring of 1986. Females farowed in the same season as that in which they were born and both farrowing groups were again closed after this single cross-classification.

Pigs born in the fall of 1985 and spring of 1986 represent the base generation for the FFG and SFG, respectively. The base generation was composed of F' males and females. Males were randomly assigned to be allowed either ad libitum or a limited intake (83% of predicted ad libitum). Each intake group was composed of 36 males per farrowing group tested from 36 to 104 kg. The six fastest gaining boars under limited intake sired generation one of a line (L) in which selection was for increased daily gain from 36 through 104 kg (ADG) at limited intake. The six fastest gaining boars under ad libitum intake sired generation one of a line (F) in which selection was for increased ADG at ad libitum intake. The F line was a continuation of F', except that the period under which selection occurred changed from 9 wk of age through 100 kg to 36 through 104 kg. Six average gaining boars from the ad libitum fed group sired generation one of an unselected control (C).

All females were tested under ad libitum intake and average females from each litter were randomly assigned to either the C, F or L line. Lines were closed with the mating of the selected base generation males and females.

Selection and Management

Selection was practiced only on males from 36 kg through 104 kg. Barrows and gilts were penned together by line and tested from 9 wk of age through 100 kg. Response to selection was measured in the barrows and gilts, thus response was measured over a slightly different range than that under which selection occurred. No intentional selection was made among females of any of the three lines. Management of the barrows and gilts is described in more detail below.

A total of five generations of selection was practiced. Pigs born in the fall of 1990 and the spring of 1991 represent the fifth generation of response. Boars and gilts were replaced after producing one litter, resulting in a generation interval of 1 yr. Each line was maintained with six boars and 25 females. The replacements were selected from 36 males and 75 to 100 females tested per line (Table 1). One or two males per litter were randomly chosen for testing at 21 d of age and the remaining males were castrated.

The growing-finishing barrows and gilts were housed in two adjacent confinement barns. All boars were tested in the same barn. Most of the barrows and gilts were tested in a second barn, but a few pens were contained in the same building as the boars. Mixed pens of barrows and gilts consisted of 16 to 18 pigs from the same line and all littermates were penned together whenever possible. The barns consisted of solid concrete flooring with a narrow flush gutter. Climate control consisted of modified sides that could be opened during warm weather, a mist cooling system and heaters. Pigs were moved into the barns at eight wk of age. Barrows and gilts were given a one wk adjustment period prior to beginning test at nine wk of age. Boars from the C and F lines were penned by line at 8 or 9 wk of age; individuals began test when they reached an on-test weight of 36 kg (ONWT). Boars from the L line were placed in individual pens when they reached 31 kg, which allowed at least a one wk adjustment period prior to reaching ONWT.

Barrows and gilts were switched from growing to finishing phase diets when the pen average weight was 54 kg. Growing phase diets were balanced to .75%

TABLE 1

NUMBER OF LITTERS BORN, BARROWS AND GILTS TESTED, PENS OF BARROWS AND GILTS TESTED AND CARCASS BARROWS SLAUGHTERED BY FARROWING GROUP-LINE-GENERATION

| FARROW GROUP[a] | LINE[b] | GENERATION | LITTERS BORN | BARROWS TESTED | GILTS TESTED | PENS[c] | CARCASS BARROWS |
|---|---|---|---|---|---|---|---|
| FALL | C | 1 | 26 | 48 | 75 | 8 | - |
| | | 2 | 22 | 25 | 87 | 7 | - |
| | | 3 | 28 | 35 | 77 | 7 | 19 |
| | | 4 | 26 | 38 | 91 | 8 | 21 |
| | | 5 | 25 | 50 | 82 | 7 | 20 |
| | F | 0 | 47 | 100 | 186 | 17 | - |
| | | 1 | 27 | 47 | 88 | 9 | - |
| | | 2 | 28 | 64 | 84 | 9 | - |
| | | 3 | 27 | 38 | 100 | 9 | 25 |
| | | 4 | 27 | 46 | 79 | 8 | 24 |
| | | 5 | 26 | 44 | 84 | 8 | 17 |
| | L | 1 | 26 | 42 | 95 | 9 | - |
| | | 2 | 24 | 39 | 83 | 8 | - |
| | | 3 | 27 | 43 | 86 | 8 | 20 |
| | | 4 | 23 | 36 | 92 | 8 | 16 |
| | | 5 | 25 | 48 | 86 | 9 | 21 |
| SPRING | C | 1 | 24 | 46 | 89 | 9 | - |
| | | 2 | 25 | 36 | 89 | 8 | - |
| | | 3 | 27 | 40 | 89 | 9 | 20 |
| | | 4 | 25 | 50 | 82 | 8 | 20 |
| | | 5 | 26 | 69 | 98 | 10 | 24 |
| | F | 0 | 51 | 96 | 171 | 18 | - |
| | | 1 | 25 | 39 | 88 | 8 | - |
| | | 2 | 20 | 36 | 70 | 7 | - |
| | | 3 | 26 | 36 | 100 | 7 | 17 |
| | | 4 | 26 | 44 | 84 | 8 | 15 |
| | | 5 | 26 | 34 | 62 | 7 | 17 |
| | L | 1 | 23 | 36 | 90 | 8 | - |
| | | 2 | 21 | 31 | 84 | 7 | - |
| | | 3 | 25 | 54 | 74 | 8 | 23 |
| | | 4 | 26 | 48 | 86 | 8 | 22 |
| | | 5 | 26 | 43 | 82 | 8 | 20 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.
[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.
[c]Pens consisted of 15 to 18 barrows and gilts from the same line.

lysine (about 15.5% crude protein) and finishing phase diets were balanced to .62% lysine (about 14.5% crude protein). Nutritional trials were superimposed on all but three of the generation-farrowing group (GFG) combinations. Each GFG contained a control corn-soybean diet and two or three experimental diets. The experimental diets may have varied slightly from the lysine and crude protein levels described above, depending on the nature of the nutritional treatment. All diets were assigned in a factorial arrangement with lines.

After a pig in a given pen reached 100 kg, all individuals in that pen were weighed weekly. Individuals were removed from test the first wk they weighed at least 100 kg. Upon removal from test, backfat was measured at the first rib, last rib and last lumbar vertebrae using an A-mode ultrasonic instrument. The average of the three measurements was adjusted to 104 kg. Total pen feed consumption was also recorded for the growing and finishing phases.

Two females were chosen as replacements from each litter when the first gilt from that litter was removed from test. The gilts within each litter were ranked highest to lowest based on weight and the two middle ranking females were kept as replacements. When an odd number of gilts occurred in a litter, the middle ranking gilt and the one that was nearest her in weight were kept.

Boars from L were individually fed at a level that was 83% of predicted ad libitum intake. Predicted intake levels were based on feeding trails with barrows from the F' line (Woltmann et al., 1992). Feed restriction of L boars began at ONWT. This limited level of intake eliminated most of the variation in average daily intake among L boars over the period which they were tested. The boars were fed the finishing diet described above, containing .62% lysine.

Each generation 36 L males were tested, each in an individual pen that was approximately 6 $m^2$. Boars were weighed weekly and intake levels were adjusted weekly based on the new weight. Daily gain (kg/d) was measured through the first weekly weighing of 104 kg or greater (OFFWT). The six fastest gaining males were selected to sire the next generation.

In all generations beyond the base, 36 C and F boars were also tested in each GFG. They were housed in pens of 12 and both lines were allowed ad libitum access to feed. Daily gain was measured over the same weight range as L. Each pen was weighed weekly until all boars within that pen reached ONWT. Boars were individually removed from test and backfat ultrasonically measured at OFFWT, as described for barrows and gilts. In F, the six fastest gaining boars were selected. While for C, the six average or middle ranking boars were selected.

The C and F boars were all fed the control corn-soybean meal finishing diet once all boars within that pen reached ONWT. Pen feed intake was measured from the time the last boar reached ONWT until all males were removed from test. Due to the weight range of the boars within a pen when the last boar reached ONWT (usually 15 to 25 kg), the feed intake data were of little value and is not directly comparable to L. The L boars were also fed the control finishing diet throughout the test period. Feed:gain and average daily intake were calculated based on weekly feed intakes and body weights for each boar.

In the fifth generation additional information was taken at off-test. Movement and front-end soundness of barrows and gilts were subjectively scored by two independent scorers. A soundness score was given based on the shape of the front leg, angle of the shoulder and size of the toes. The movement score was based on relative freedom of movement and was evaluated independent of soundness. The scoring system used was adapted from Rothschild and Christian (1988). Possible scores for movement and structure ranged from 1 (unable to move) to 9 (ideal). For a more detailed description of the scores see Table 2.

In situ testicle volume was measured for generation five boars. A caliper was used to measure length and width across both testicles at 150 days of age and

TABLE 2

DESCRIPTION OF SOUNDNESS AND MOVEMENT SCORES[a]

| SCORE[b] | DESCRIPTION OF FRONT-END SOUNDNESS | DESCRIPTION OF FRONT MOVEMENT |
|---|---|---|
| 1 | unable to get up due to poor front structure | unable to get up or move |
| 2 | able to stand with much difficulty, unable to walk | able to move only with help |
| 3 | bent kneed, shoulder angle greater than 90°, small and/or uneven toes | moves with severe resticition, very small strides |
| 5 | straight front legs, average toe size, shoulder angle slightly greater than 90° | moves with a moderate degree of restriction, strides somewhat small and choppy |
| 7 | shoulder angle very near 90°, sloping front leg (C-shaped), above average toe size | moves with little restricition, moderately long smooth strides |
| 9 | ideal, large toe size, shoulder angle 90°, sloping front leg | ideal, no resticition, very long smooth strides |

[a]Adopted from Rothschild and Christian (1988).
[b]Scores of 4, 6 and 8 are degrees of soundness or movement relative to the score either side of them.

OFFWT. Testicular volume was estimated by $(\text{width}/2)^2$ x length (Toelle et al., 1984).

Boars and gilts retained as replacements were moved from the confinement barns to soil lots at OFFWT. Gilts were hand mated at approximately 8 months of age. Breeding records were kept to allow for the calculation of conception rate. Each male was generally mated to 4 or 5 females. A computer program that calculated the inbreeding coefficient of each individual and all potential matings was used to help avoid matings producing high levels of inbreeding.

Due to the limit in farrowing facilities, females were bred until enough matings were made to fill the facility. A short break was taken before the next group was bred. A total of four groups were bred, generally over a 6 to 7 wk period. Within each group the number of C, F and L litters was kept as uniform as possible. Nutritional trials were also imposed on the gestating females during most of the GFG. Gilts were fed 2.3 kg daily during gestation and allowed ad libitum access to feed while nursing litters.

Gilts were farrowed in crates on wooden floors. At approximately one wk of age the sow and litter was removed from the farrowing house to an individual nursery pen. Pen floors were solid concrete and each pen contained an indoor and outdoor area that allowed for sow and litter to be locked inside during cold weather. At three wk of age creep feed was made available to the piglets. At 42 d post-farrowing the sow was removed and the litter remained in the nursery pen until being transferred to the growing-finishing barn at eight wk of age. Individual piglet weights were recorded at birth, 21 and 42 d of age. Females were weighed at breeding, 109 days of gestation and weaning. Table 1 summarizes the number of litters born each GFG.

Carcass data were collected for generations 3, 4 and 5. One randomly selected barrow per litter was slaughtered after removal from test. A commercial facility slaughtered the barrows and the right side of each carcass was transported to the Oklahoma State Meat Laboratory. Loin eye area, carcass length, quality scores, backfat measurements at the shoulder, last rib and last lumbar vertebra and fat depth measurements at the tenth rib were collected. Each carcass was given a subjective muscling score of 1 to 3 (1=thin, 2=average, 3=thick). The half carcass was broken down into the four major wholesale cuts of the ham, loin, boston butt and picnic. Excess fat was removed and weights were taken on each of the closely trimmed wholesale cuts. Cutability was defined as the proportion of the closely trimmed major wholesale cuts in the chilled carcass.

The average of the three backfat measurements and loin eye area were adjusted to 104 kg. Carcass grade was predicted by (4 x 10th rib backfat) - muscle score. In addition, total carcass lean was predicted using loin eye area, carcass weight and fat depth (Grisdale et al., 1984). Lean gain per day on test was estimated using the same three measurements plus on-test weight and days on test (Grisdale et al., 1984).

## Selection Differentials

Selection differentials for ADG were calculated by deviating each selected individual's record from the appropriate generation-farrowing group-line-sex subclass mean. Unweighted selection differentials for each individual were proportionately weighted by the number of progeny that had an ADG record. The average weighted selection differential for each farrowing group-line-sex subclass was added to the cumulative total from the previous generation (WCSD). Boar and gilt differentials were calculated separately. The within subclass differentials were standardized by the within line phenotypic SD for ADG.

Statistical Analysis

Traits examined from generations zero through five included birth weight (BW), 21-d weight (D21W), 42-d weight (D42W), ADG for the growing (DG1) and finishing period (DG2), and overall (DG), probed backfat adjusted to 104 kg (APBF) and d to 104 kg (D104). Pen data included daily feed intake for the growing (FI1) and finishing period (FI2), overall daily feed intake (FI), feed efficiency for the growing (FG1) and finishing period (FG2) and overall feed efficiency (FG). Traits of the dam studied in generations zero through four included number born (NB), total litter weight at birth (LWB), number alive at 21 d (N21D), total litter weight at 21 d (LW21D), number alive at 42 d (N42D) and total litter weight at 42 d (LW42D).

A number of traits were only studied in latter generations. These included the following carcass traits in generations 3, 4 and 5: backfat adjusted to 104 kg (ACBF), loin eye area adjusted to 104 kg (LEA), percent carcass lean (PLEAN), lean gain per day on test (LDG), carcass grade, cutability (CUT), length and marbling score (MSCORE). First and second service conception rate, defined as the percentage of gilts exposed to a boar that farrowed a litter, were analyzed as traits of the dam for generations 2, 3 and 4. Movement (MOVE) and structure (STRU) of barrows and gilts at OFFWT and testicular volume at 150 d of age (TV150) and off test (TVOT) were examined in generation five only.

A number of statistical models were used to analyze the traits of interest. Refer to appendix Tables 30 through 38 for the sources of variation in each of the models. The effects of line, generation, farrowing group and sex were cross-classified variables when included in the model. Superimposed experimental diets varied between generation-farrowing group subclasses and thus diet were considered to be nested within generation-farrowing group. The General Linear Models procedure in SAS (1985) was used. A full model was analyzed for each trait, but the final model included only sources of variation that were considered statistically significant. All main effects and only the interaction effects that had significance levels less than 0.20 were kept in the final model. All non-significant interactions (P>.20) were removed from the final model as sources of variation. The residual mean square error was used as the error term.

Means for base generation traits of the pig were estimated separately, because C, F and L were established from a single base population. The effects of farrowing group, sex and diet and all appropriate interactions were included in the statistical model; however, the effect of sex was not included in the analyses of pen data. The final models used were determined as described above. The spring and fall farrowing group least-squares means were considered the base generation level of performance for all three lines.

Analyses of trends over time are of the most interest for the traits that were collected each generation. Specific comparisons are of interest for those traits examined only in later generations. Comparisons of interest within each farrowing group were C vs. F, C vs. L and F vs. L. These comparisons were non-orthogonal and were tested using Bonferroni t statistics (Gill, 1986).

Movement and structure scores collected in generation five were arbitrarily grouped into three soundness classes. A pig was considered unsound if assigned a score less than 5, moderately sound for scores of 5 and 5.5 and sound if given a score of 6 or greater. A chi-square analysis (SAS, 1985) was performed to test for the independence of soundness class and line. Movement was averaged over farrowing group since the interaction of line and farrowing group was non-significant (P=.68), but within farrowing group analyses were performed for structure. In addition, phenotypic partial correlations across farrowing group were calculated between DG, APBF, MOVE and STRU.

Regression methods were used to estimate realized response per WCSD and generation, except those measured only in specific generations. Generation-line-farrowing group least-squares means from analysis of the final models were used as the measurements of response. Contemporary group environmental effects were corrected for by deviating the select from the control line least-squares means. Response was estimated by regressing the response deviation on one-half of the male WCSD or generation (Falconer, 1989). The WCSD was not corrected for contemporary group effects in either F or L due to the lack of a limit-fed control. In addition, unintentional gilt selection was not accounted for in the regressions because of the intake level differences between L-line boars and gilts. Response was analyzed both within and across farrowing group. The presented standard errors are regression estimates from the across farrowing group analysis. These standard errors do not account for genetic drift and thus may underestimate error (Hill, 1972).

Realized co-heritabilities between DG and the other traits are standardized measures of correlated response (Yamada, 1968). They are equal to $h_{DG}h_{CT}r_A$, where $h_{DG}$ and $h_{CT}$ are the square roots of heritability for DG and the correlated trait, respectively. The genetic correlation between DG and the correlated trait is represented by $r_A$. Co-heritabilities were calculated by standardizing the across farrowing group regression coefficients of the correlated trait on WCSD. The regressions were standardized by multiplication of the coefficients by the ratio of the phenotypic SD of DG to the SD of the correlated trait. For pen data (FG, FG1, FG2, FI, FI1, FI2) the phenotypic SD was actually a standard error. This is because a pen observation is a mean of 16.3 pigs (average number of pigs per pen). The root mean square, which was used to estimate the phenotypic standard error, was multiplied by the square root of 16.3 to estimate the SD. After correction, the SD estimates for FG and FI agree closely with estimates of individually fed pigs at the same research station (Woltmann, 1989). Standard errors of the co-heritabilities were estimated by standardizing the standard errors for the across generation regressions using the same procedures. The estimates of the co-heritabilities standard errors do not account for genetic drift.

Response to selection for traits contributing directly to LTGR and LTFC was also quantified by a point estimate in generation five. A within generation five least-squares analysis was performed on DG, APBF, FG and FI. The models fit for each trait were equivalent to those described above with the exception that the effects of generation were not included. Refer to appendix Table 34 for the specific sources of variation. The least-squares means for line were contrasted to determine line differences (SAS, 1985).

## Results and Discussion

### Inbreeding

Response to selection was not corrected for inbreeding. The level of inbreeding remained relatively low during the study (Table 3). In addition, differences in actual inbreeding levels remained small between the control and selected lines within each generation. Generation five barrows and gilts from all three lines had average inbreeding levels that were below 10% for the SFG and FFG. Inbreeding coefficients at this relatively low level will only slightly depress ADG (Johnson, 1990). For each inbreeding increase of 10% in the pig daily gain is expected to decrease by .023 kg/d and the inbreeding level of the dam has no effect on gain.

Inbreeding accumulation is expected to increase at a rate of about 2.5% per generation based on an effective population size of 19 (6 males and 25 females). Generation five inbreeding is 3 to 5% below the expected level, mainly due to the method of mating used to avoid inbreeding. However, most of the advantage in

TABLE 3

PERCENT INBREEDING FOR THE TESTED BARROWS AND GILTS AND AND FEMALES PRODUCING LITTERS BY FARROWING GROUP-LINE-GENERATION

| FARROW GROUP[a] | LINE[b] | GENERATION | BARROWS AND GILTS | FEMALES PRODUCING LITTERS |
|---|---|---|---|---|
| FALL | C | 1 | 0.71 | 0.00 |
| | | 2 | 1.87 | 1.70 |
| | | 3 | 4.59 | 2.73 |
| | | 4 | 6.76 | 4.45 |
| | | 5 | 8.86 | 7.18 |
| | F | 0 | 0.00 | * |
| | | 1 | 0.00 | 0.00 |
| | | 2 | 0.76 | 0.00 |
| | | 3 | 4.21 | 1.25 |
| | | 4 | 5.83 | 3.85 |
| | | 5 | 8.44 | 5.66 |
| | L | 1 | 0.00 | 0.00 |
| | | 2 | 0.89 | 0.00 |
| | | 3 | 4.48 | 0.25 |
| | | 4 | 6.13 | 4.62 |
| | | 5 | 9.34 | 6.36 |
| SPRING | C | 1 | 0.74 | 0.00 |
| | | 2 | 3.00 | 1.04 |
| | | 3 | 5.24 | 1.63 |
| | | 4 | 7.27 | 5.54 |
| | | 5 | 9.65 | 6.31 |
| | F | 0 | 0.00 | * |
| | | 1 | 0.49 | 0.00 |
| | | 2 | 0.77 | 0.62 |
| | | 3 | 4.39 | 0.95 |
| | | 4 | 5.42 | 3.58 |
| | | 5 | 9.16 | 5.51 |
| | L | 1 | 0.84 | 0.00 |
| | | 2 | 0.27 | 0.60 |
| | | 3 | 3.48 | 0.38 |
| | | 4 | 4.92 | 3.39 |
| | | 5 | 7.49 | 5.27 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

*Females from previous study were use to form the base generation, predicted inbreeding based on effective population size is 7.2% for the fall farrowing group and 9.0% for the spring farrowing group.

lowered inbreeding was the result of the first two generations when inbreeding could be avoided. For the final three generations inbreeding increased at a rate very near the predicted rate.

## Boars

Means for performance characteristics of C, F and L boars are presented in Table 4. Daily intake and feed:gain are not given for C and F due to the method of placing boars within a pen on test. On-test dates within a pen varied as much as 3 to 4 wk. This often resulted in a weight range of 20 kg or more when measurement of feed consumption began and because of this feed intake is not directly comparable across lines.

Daily intake levels of L boars were constant across farrowing group and generations (Table 4). The level of restricted feeding employed eliminated most of the variation in daily intake over the weight period which restriction occurred, indicating the level to which boars were restricted was sufficient. The variation that did exist resulted from occasional refusals by a small number of boars and to some extent differences in the time and weight range over which boars were tested.

Daily lysine intake for L boars was below recommended levels (NRC, 1988) throughout most of the test period (Figure 1) due to the restricted level of intake imposed and the relatively low lysine content of the diet. They graphed requirements represent those of barrows and gilts. These daily requirements would be even higher for boars of the same genetic line. The low level of lysine and/or protein in the L boar diet may have not provided an adequate nutritional environment to allow lean growth variation to be fully expressed. Thus potential response to selection for lean growth may have not been fully realized.

The breeding objective in L was LTFC, utilizing a method of restriction that

TABLE 4

MEANS FOR PERFORMANCE CHARACTERISTICS OF BOARS BY FARROWING GROUP-LINE-GENERATION

| FARROW GROUP[a] | LINE[b] | GENERATION | DAILY GAIN | ADJUSTED BACKFAT (cm) | DAYS TO 104.5 KG | DAILY INTAKE | FEED:GAIN |
|---|---|---|---|---|---|---|---|
| FALL | C | 1 | 0.97 | 2.95 | 153.3 | | |
| | | 2 | 0.93 | 2.89 | 161.8 | | |
| | | 3 | 0.99 | 2.46 | 154.4 | | |
| | | 4 | 0.98 | 2.52 | 156.0 | | |
| | | 5 | 0.97 | 2.62 | 157.3 | | |
| | F | 0 | 0.94 | 2.74 | 160.8 | | |
| | | 1 | 0.95 | 2.81 | 158.7 | | |
| | | 2 | 0.92 | 3.04 | 157.3 | | |
| | | 3 | 1.02 | 2.53 | 153.0 | | |
| | | 4 | 1.02 | 2.67 | 151.9 | | |
| | | 5 | 1.01 | 2.76 | 153.6 | | |
| | L | 0 | 0.84 | 2.53 | 169.8 | 2.57 | 3.06 |
| | | 1 | 0.81 | 2.77 | 170.8 | 2.56 | 3.17 |
| | | 2 | 0.81 | 2.80 | 174.1 | 2.56 | 3.18 |
| | | 3 | 0.86 | 2.07 | 172.2 | 2.57 | 3.00 |
| | | 4 | 0.87 | 2.27 | 160.6 | 2.58 | 2.88 |
| | | 5 | 0.85 | 2.24 | 170.4 | 2.55 | 2.99 |
| SPRING | C | 1 | 1.01 | 3.09 | 157.1 | | |
| | | 2 | 0.97 | 3.19 | 153.9 | | |
| | | 3 | 0.93 | 2.81 | 154.2 | | |
| | | 4 | 0.90 | 2.87 | 164.0 | | |
| | | 5 | 0.92 | 2.86 | 159.9 | | |
| | F | 0 | 1.02 | 3.02 | 156.5 | | |
| | | 1 | 1.04 | 3.23 | 150.2 | | |
| | | 2 | 1.02 | 3.19 | 153.9 | | |
| | | 3 | 0.98 | 2.73 | 152.2 | | |
| | | 4 | 0.99 | 2.93 | 155.3 | | |
| | | 5 | 1.05 | 3.08 | 147.1 | | |
| | L | 0 | 0.84 | 2.53 | 169.8 | 2.57 | 3.06 |
| | | 1 | 0.85 | 3.04 | 168.9 | 2.57 | 3.05 |
| | | 2 | 0.85 | 2.65 | 168.9 | 2.56 | 3.00 |
| | | 3 | 0.89 | 2.40 | 159.6 | 2.55 | 2.87 |
| | | 4 | 0.90 | 2.42 | 160.7 | 2.58 | 2.88 |
| | | 5 | 0.92 | 2.45 | 157.4 | 2.57 | 2.80 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

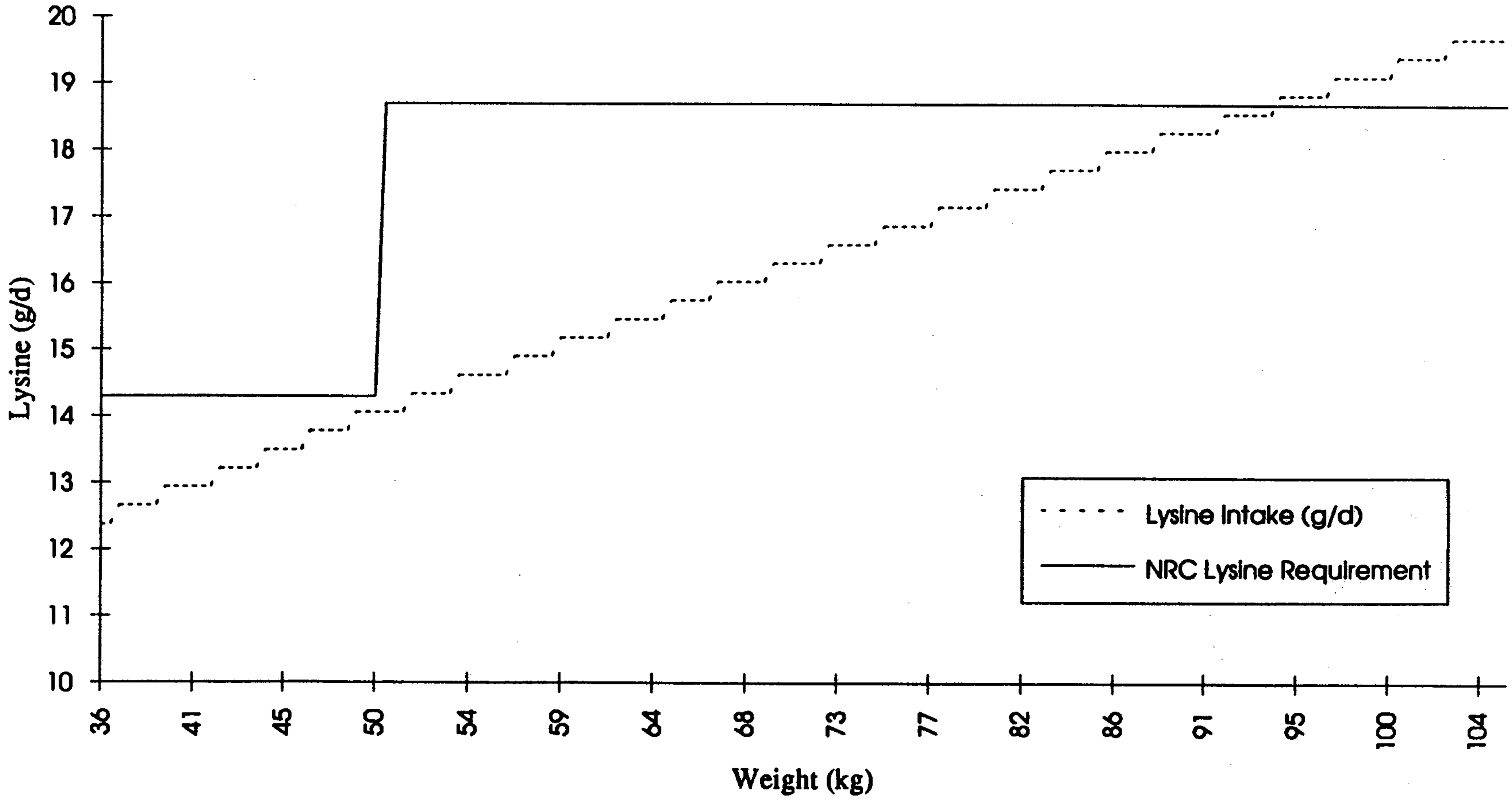


Figure 1. Dietary Daily Lysine Intake of L Boars

can be best described as a weight-scale feeding system, since boars were scale fed over a weight constant range of 36 to 104 kg. Fowler et al. (1976) suggested a time-scale feeding system and McPhee et al. (1988) used this method to select for increased weight of ham lean. Under the time-scale method all pigs are given the same amount of food over a time constant period, thus the daily intake level allowed is determined by time on test. In contrast, the daily ration of food is determined by the weight of the pig when using the weight-scale system. Variation in total food intake while on test is not eliminated using the weight-scale method, however, variation relative to body weight is removed.

The most efficient individuals will be selected under both the weight- and time-scale methods. Examining the ratio of feed:gain over the entire test period, one component is constant in each method. The time-scale system holds total food intake constant, resulting in a perfect correlation between gain and efficiency. The weight-scale system keeps total weight gain while on test nearly constant, allowing for some variation due to the method of initiating and ending test. Those that gain most rapidly will be on test for a shorter period and thus consume less total feed. The correlation between gain and efficiency is expected to be high, but not perfect as is the case of the time-scale method. A high inverse relationship was seen in the L line means for DG and FE in both farrowing groups (Table 4).

The relationship between lean growth and lean growth efficiency under scale feeding is very similar to the relationship that exists between total body growth and efficiency. To better understand this relationship the ratio of feed:lean gain must be examined. Feed remains constant for the time-scale feeding method, thus ranking individuals on lean growth is equivalent to ranking them on lean efficiency . The relationship under the weight-scale method utilized in the present study is slightly more complicated. Neither feed nor lean gain are constant; however, body weight gain remained nearly constant. The strength of this relationship is dependent on the correlation between body weight gain and lean gain under the limited intake level. This correlation is expected to increase utilizing a standardized intake because lean deposition is more efficient than fat deposition, thus those gaining body weight more rapidly are gaining lean at a faster rate.

Gilts

Gilt ADG and backfat were measured under ad libitum intake from 9 wk of age through 100 kg in C, F and L (Table 5). Intake and efficiency of the gilts cannot be calculated since barrows and gilts were penned together for testing. Two gilts from each litter that were representative for growth rate were selected as potential replacements. Thus, any selection pressure placed on the females was unintentional. This was reflected in the small deviations of those selected to be potential replacements from their contemporary group means (Table 5). However, the deviation of those females producing the next generation unweighted (Table 6) or weighted (Table 7) by the number of offspring they contributed to that generation was larger in most subclasses. Thus unintentional selection took place from the time potential replacements were selected to when the gilts became pregnant. This small amount of selection suggests gilts that gained more rapidly tended to reach sexual maturity earlier and thus were more likely to be mated and conceive.

Selection

Selection was intentionally practiced only in F and L boars. Within generation unweighted and weighted deviations are presented in Tables 6 and 7, respectively. Each deviation or individual selection differential was weighted by the number of offspring out of that boar or gilt that had a DG record the following generation. Weighted and unweighted deviations were numerically similar for all

TABLE 5

LEAST-SQUARES MEANS FOR PERFORMANCE CHARACTERISTICS OF GILTS BY FARROWING GROUP-LINE-GENERATION

| FARROW GROUP[a] | LINE[b] | GENERATION | DAILY GAIN | DEVIATION (KG/D) OF THOSE SELECTED AS REPLACEMENTS[c] | ADJUSTED BACKFAT (cm) |
|---|---|---|---|---|---|
| FALL | C | 1 | 0.85 | 0.002 | 3.09 |
| | | 2 | 0.83 | -0.007 | 3.18 |
| | | 3 | 0.90 | 0.018 | 2.98 |
| | | 4 | 0.89 | 0.038 | 2.84 |
| | | 5 | 0.87 | | 3.01 |
| | F | 0 | 0.82 | | 3.15 |
| | | 1 | 0.84 | 0.006 | 3.06 |
| | | 2 | 0.84 | -0.006 | 3.28 |
| | | 3 | 0.89 | 0.016 | 2.97 |
| | | 4 | 0.90 | -0.018 | 2.92 |
| | | 5 | 0.86 | | 3.13 |
| | L | 1 | 0.82 | 0.003 | 3.10 |
| | | 2 | 0.81 | 0.014 | 3.15 |
| | | 3 | 0.82 | 0.018 | 2.77 |
| | | 4 | 0.84 | -0.042 | 2.55 |
| | | 5 | 0.81 | | 2.90 |
| SPRING | C | 1 | 0.85 | 0.001 | 3.41 |
| | | 2 | 0.79 | 0.007 | 3.38 |
| | | 3 | 0.84 | 0.008 | 3.30 |
| | | 4 | 0.80 | 0.008 | 3.43 |
| | | 5 | 0.85 | | 3.59 |
| | F | 0 | 0.85 | | 3.24 |
| | | 1 | 0.87 | -0.006 | 3.53 |
| | | 2 | 0.81 | 0.007 | 3.24 |
| | | 3 | 0.88 | -0.004 | 3.17 |
| | | 4 | 0.87 | 0.021 | 3.37 |
| | | 5 | 0.93 | | 3.48 |
| | L | 1 | 0.84 | 0.000 | 3.41 |
| | | 2 | 0.81 | 0.015 | 3.26 |
| | | 3 | 0.86 | 0.006 | 3.13 |
| | | 4 | 0.88 | -0.013 | 3.17 |
| | | 5 | 0.87 | | 3.32 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]The deviation of those selected as potential replacement females versus the average of all females.

TABLE 6

UNWEIGHTED CUMULATIVE SELECTION DIFFERENTIALS BY FARROWING GROUP-LINE

| FARROW GROUP[a] | LINE[b] | GENER-ATION[c] | UNWEIGHTED DEVIATION FEMALE | UNWEIGHTED DEVIATION MALE | CUMULATIVE SELECTION DIFFERENTIAL FEMALE | CUMULATIVE SELECTION DIFFERENTIAL MALE |
|---|---|---|---|---|---|---|
| FALL | C | 0 | 0.004 | - 0.020 | 0.004 | -0.020 |
| | | 1 | 0.021 | - 0.006 | 0.025 | -0.026 |
| | | 2 | 0.023 | 0.016 | 0.048 | -0.010 |
| | | 3 | 0.032 | 0.006 | 0.080 | -0.004 |
| | | 4 | 0.031 | - 0.009 | 0.111 | -0.013 |
| | F | 0 | 0.013 | 0.101 | 0.013 | 0.101 |
| | | 1 | 0.019 | 0.145 | 0.032 | 0.246 |
| | | 2 | 0.038 | 0.111 | 0.070 | 0.357 |
| | | 3 | 0.019 | 0.133 | 0.089 | 0.490 |
| | | 4 | -0.025 | 0.127 | 0.064 | 0.617 |
| | L | 0 | 0.007 | 0.036 | 0.007 | 0.036 |
| | | 1 | 0.005 | 0.062 | 0.012 | 0.098 |
| | | 2 | 0.019 | 0.044 | 0.031 | 0.142 |
| | | 3 | 0.023 | 0.054 | 0.054 | 0.196 |
| | | 4 | -0.041 | 0.052 | 0.013 | 0.248 |
| SPRING | C | 0 | -0.007 | 0.018 | -0.007 | 0.018 |
| | | 1 | 0.002 | 0.014 | -0.005 | 0.032 |
| | | 2 | 0.019 | 0.004 | 0.014 | 0.036 |
| | | 3 | 0.004 | 0.022 | 0.018 | 0.058 |
| | | 4 | 0.007 | 0.046 | 0.025 | 0.104 |
| | F | 0 | 0.018 | 0.153 | 0.018 | 0.153 |
| | | 1 | 0.018 | 0.130 | 0.036 | 0.283 |
| | | 2 | 0.006 | 0.110 | 0.042 | 0.393 |
| | | 3 | 0.016 | 0.121 | 0.058 | 0.514 |
| | | 4 | 0.031 | 0.142 | 0.089 | 0.656 |
| | L | 0 | 0.020 | 0.036 | 0.020 | 0.036 |
| | | 1 | 0.004 | 0.073 | 0.024 | 0.109 |
| | | 2 | 0.038 | 0.054 | 0.062 | 0.163 |
| | | 3 | 0.005 | 0.059 | 0.067 | 0.222 |
| | | 4 | -0.008 | 0.058 | 0.059 | 0.280 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]Generation represents the amount of selection that occurred in the sow.

TABLE 7

WEIGHTED CUMULATIVE SELECTION DIFFERENTIALS BY FARROWING GROUP-LINE

| FARROW GROUP[a] | LINE[b] | GENERATION[c] | WEIGHTED DEVIATION FEMALE | WEIGHTED DEVIATION MALE | CUMULATIVE SELECTION DIFFERENTIAL FEMALE | CUMULATIVE SELECTION DIFFERENTIAL MALE |
|---|---|---|---|---|---|---|
| FALL | C | 0 | 0.021 | - 0.020 | 0.021 | -0.020 |
| | | 1 | 0.033 | - 0.008 | 0.054 | -0.028 |
| | | 2 | 0.034 | 0.016 | 0.088 | -0.012 |
| | | 3 | 0.035 | 0.007 | 0.123 | -0.005 |
| | | 4 | 0.029 | - 0.004 | 0.152 | -0.009 |
| | F | 0 | 0.017 | 0.107 | 0.017 | 0.107 |
| | | 1 | 0.021 | 0.143 | 0.038 | 0.250 |
| | | 2 | 0.037 | 0.110 | 0.075 | 0.360 |
| | | 3 | 0.023 | 0.131 | 0.098 | 0.491 |
| | | 4 | -0.030 | 0.128 | 0.068 | 0.619 |
| | L | 0 | 0.000 | 0.036 | 0.000 | 0.036 |
| | | 1 | 0.000 | 0.064 | 0.000 | 0.100 |
| | | 2 | 0.016 | 0.046 | 0.016 | 0.146 |
| | | 3 | 0.024 | 0.055 | 0.040 | 0.201 |
| | | 4 | -0.040 | 0.052 | 0.000 | 0.253 |
| SPRING | C | 0 | 0.001 | 0.006 | 0.001 | 0.006 |
| | | 1 | -0.007 | 0.013 | -0.006 | 0.019 |
| | | 2 | 0.015 | 0.003 | 0.009 | 0.022 |
| | | 3 | 0.009 | 0.022 | 0.018 | 0.044 |
| | | 4 | 0.012 | 0.050 | 0.030 | 0.094 |
| | F | 0 | 0.010 | 0.158 | 0.010 | 0.158 |
| | | 1 | 0.011 | 0.121 | 0.021 | 0.279 |
| | | 2 | 0.001 | 0.108 | 0.022 | 0.387 |
| | | 3 | 0.014 | 0.121 | 0.036 | 0.508 |
| | | 4 | 0.035 | 0.154 | 0.071 | 0.662 |
| | L | 0 | 0.028 | 0.037 | 0.028 | 0.037 |
| | | 1 | 0.000 | 0.069 | 0.028 | 0.106 |
| | | 2 | 0.032 | 0.057 | 0.060 | 0.163 |
| | | 3 | 0.006 | 0.064 | 0.066 | 0.227 |
| | | 4 | -0.011 | 0.054 | 0.055 | 0.281 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]Generation represents the amount of selection that occurred in the sow.

generation-farrowing group-line subclasses. Male and female WCSD are presented separately (Tables 6 and 7). Total unintentional selection in the gilts was zero for L-FFG and was about 10% of the male WCSD for L-SFG, F-FFG and F-SFG. Unintentional female selection was not accounted for in the WCSD used in the regressions that measured response per WCSD (e.g., Table 13). Because of the differences in allowed intake level between L boars and gilts the measured unintentional selection cannot be assumed to be a direct function of the standard limited intake under which the males were selected.

Weighted differentials were at least twice as high in F, as compared to L (Table 7); however, the phenotypic SD for DG under ad libitum intake was twice as large as the SD under the restricted level employed. When standardized, the relative amount of total selection realized was similar across line and farrowing group (Table 8). The standardized male WCSD were 6.8, 7.3, 5.5 and 6.1 for F-FFG, F-SFG, L-FFG and L-SFG, respectively. Total realized selection was assumed to be one-half of the standardized WCSD, since unintentional female selection was not accounted for. Similar differences in variation due to feeding level have been reported in mice. The phenotypic variation for weight gain was 2.5 times higher in a line selected under ad libitum intake, as compared to a line selected under a restricted intake (Hetzel and Nicholas, 1982) and the cumulative selection differential for gain was 50% higher in a line selected under ad libitum intake (McPhee and Trappett, 1987).

Measurement of response

Least-squares means are presented by farrowing group-line-generation for barrow and gilt growth rate and probed fat (Table 9), pen intake and efficiency (Table 10) and individual pig weight (Table 11). The corresponding probability

TABLE 8

STANDARDIZED[a] WEIGHTED CUMULATIVE SELECTION DIFFERENTIALS BY FARROWING GROUP-LINE

| FARROW GROUP[b] | LINE[c] | GENERATION[d] | STANDARDIZED WEIGHTED DEVIATION FEMALE | STANDARDIZED WEIGHTED DEVIATION MALE | STANDARDIZED CUMULATIVE DIFFERENTIAL FEMALE | STANDARDIZED CUMULATIVE DIFFERENTIAL MALE |
|---|---|---|---|---|---|---|
| FALL | C | 0 | 0.231 | - 0.220 | 0.231 | -0.220 |
| | | 1 | 0.363 | - 0.088 | 0.594 | -0.308 |
| | | 2 | 0.374 | 0.176 | 0.968 | -0.132 |
| | | 3 | 0.385 | 0.077 | 1.353 | -0.055 |
| | | 4 | 0.319 | - 0.044 | 1.672 | -0.099 |
| | F | 0 | 0.187 | 1.186 | 0.187 | 1.186 |
| | | 1 | 0.231 | 1.571 | 0.418 | 2.757 |
| | | 2 | 0.407 | 1.209 | 0.825 | 3.966 |
| | | 3 | 0.253 | 1.440 | 1.070 | 5.406 |
| | | 4 | -0.330 | 1.407 | 0.748 | 6.813 |
| | L | 0 | 0.000 | 0.783 | 0.000 | 0.783 |
| | | 1 | 0.000 | 1.391 | 0.000 | 2.174 |
| | | 2 | 0.176 | 1.000 | 0.176 | 3.174 |
| | | 3 | 0.264 | 1.196 | 0.440 | 4.370 |
| | | 4 | -0.440 | 1.130 | 0.000 | 5.500 |
| SPRING | C | 0 | 0.011 | 0.066 | 0.011 | 0.066 |
| | | 1 | -0.077 | 0.143 | -0.066 | 0.209 |
| | | 2 | 0.165 | 0.033 | 0.099 | 0.242 |
| | | 3 | 0.099 | 0.242 | 0.198 | 0.484 |
| | | 4 | 0.132 | 0.549 | 0.330 | 1.033 |
| | F | 0 | 0.110 | 1.736 | 0.110 | 1.736 |
| | | 1 | 0.121 | 1.330 | 0.231 | 3.066 |
| | | 2 | 0.011 | 1.187 | 0.242 | 4.253 |
| | | 3 | 0.154 | 1.330 | 0.396 | 5.583 |
| | | 4 | 0.385 | 1.692 | 0.781 | 7.275 |
| | L | 0 | 0.308 | 0.804 | 0.308 | 0.804 |
| | | 1 | 0.000 | 1.500 | 0.308 | 2.304 |
| | | 2 | 0.352 | 1.239 | 0.660 | 3.543 |
| | | 3 | 0.066 | 1.391 | 0.726 | 4.934 |
| | | 4 | -0.121 | 1.174 | 0.605 | 6.108 |

[a]Standardized by the within line phenotypic standard deviation of .046 for L boars and .091 for C and F boars and all gilts.

[b]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[c]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[d]Generation represents the amount of selection that occurred in the sow.

TABLE 9

LEAST-SQUARES MEANS FOR GROWTH RATE AND BACKFAT THICKNESS OF BARROWS AND GILTS BY FARROWING GROUP-LINE-GENERATION

| FARROW GROUP[a] | LINE[b] | GENERATION | DAILY GAIN | DAILY GAIN GROW[c] | DAILY GAIN FINISH[c] | ADJUSTED BACKFAT (cm) | DAYS TO 104 KG |
|---|---|---|---|---|---|---|---|
| FALL | C | 1 | 0.85 | 0.78 | 0.90 | 3.15 | 162.7 |
| | | 2 | 0.84 | 0.77 | 0.90 | 3.25 | 165.4 |
| | | 3 | 0.90 | 0.84 | 0.96 | 2.99 | 157.2 |
| | | 4 | 0.91 | 0.82 | 0.99 | 2.95 | 159.2 |
| | | 5 | 0.89 | 0.80 | 0.97 | 3.04 | 160.2 |
| | F | 0 | 0.83 | 0.79 | 0.89 | 3.21 | 168.7 |
| | | 1 | 0.85 | 0.79 | 0.90 | 3.07 | 164.1 |
| | | 2 | 0.86 | 0.79 | 0.92 | 3.35 | 163.1 |
| | | 3 | 0.91 | 0.84 | 0.97 | 3.07 | 157.6 |
| | | 4 | 0.91 | 0.81 | 1.00 | 3.09 | 157.6 |
| | | 5 | 0.88 | 0.83 | 0.93 | 3.22 | 161.6 |
| | L | 1 | 0.85 | 0.79 | 0.90 | 3.12 | 165.1 |
| | | 2 | 0.84 | 0.76 | 0.92 | 3.28 | 167.2 |
| | | 3 | 0.85 | 0.77 | 0.93 | 2.98 | 168.4 |
| | | 4 | 0.85 | 0.76 | 0.95 | 2.74 | 164.9 |
| | | 5 | 0.84 | 0.78 | 0.90 | 3.11 | 167.2 |
| SPRING | C | 1 | 0.87 | 0.77 | 0.96 | 3.48 | 161.0 |
| | | 2 | 0.81 | 0.73 | 0.87 | 3.49 | 169.3 |
| | | 3 | 0.86 | 0.79 | 0.92 | 3.46 | 158.8 |
| | | 4 | 0.82 | 0.78 | 0.86 | 3.58 | 167.2 |
| | | 5 | 0.86 | 0.79 | 0.92 | 3.74 | 162.0 |
| | F | 0 | 0.85 | 0.74 | 0.96 | 3.30 | 163.9 |
| | | 1 | 0.88 | 0.79 | 0.96 | 3.63 | 160.2 |
| | | 2 | 0.84 | 0.76 | 0.91 | 3.38 | 166.3 |
| | | 3 | 0.89 | 0.79 | 0.97 | 3.29 | 155.7 |
| | | 4 | 0.90 | 0.82 | 0.96 | 3.46 | 159.3 |
| | | 5 | 0.94 | 0.87 | 1.02 | 3.59 | 152.7 |
| | L | 1 | 0.85 | 0.83 | 0.93 | 3.56 | 163.3 |
| | | 2 | 0.82 | 0.73 | 0.91 | 3.29 | 168.2 |
| | | 3 | 0.87 | 0.78 | 0.95 | 3.25 | 158.2 |
| | | 4 | 0.88 | 0.81 | 0.95 | 3.29 | 159.6 |
| | | 5 | 0.88 | 0.82 | 0.94 | 3.47 | 157.4 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]Grow=growing phase from 9 weeks of age through 54 kg, finish=finishing phase from 54 through 100 kg.

Standard errors ranged from .007 to .010 for daily gain, .011 to .014 for daily gain grow, .009 to .014 for daily gain finish, .031 to .047 for adjusted backfat and 1.08 to 1.58 for days to 104 kg.

TABLE 10

LEAST-SQUARES MEANS FOR PEN FEED INTAKE AND EFFICIENCY OF BARROWS AND GILTS BY FARROWING GROUP-LINE-GENERATION

| FARROW GROUP[a] | LINE[b] | GENERATION | FEED: GAIN | FEED: GAIN GROW[c] | FEED: GAIN FINISH[c] | DAILY INTAKE | DAILY INTAKE GROW[c] | DAILY INTAKE FINISH[c] |
|---|---|---|---|---|---|---|---|---|
| FALL | C | 1 | 3.06 | 2.67 | 3.34 | 2.56 | 2.08 | 2.94 |
| | | 2 | 2.99 | 2.51 | 3.33 | 2.44 | 1.93 | 2.87 |
| | | 3 | 3.14 | 2.66 | 3.49 | 2.78 | 2.21 | 3.23 |
| | | 4 | 2.99 | 2.56 | 3.33 | 2.69 | 2.09 | 3.24 |
| | | 5 | 2.95 | 2.65 | 3.17 | 2.60 | 2.12 | 3.02 |
| | F | 0 | 3.09 | 2.71 | 3.37 | 2.52 | 2.14 | 2.93 |
| | | 1 | 3.07 | 2.65 | 3.38 | 2.55 | 1.97 | 3.16 |
| | | 2 | 3.04 | 2.61 | 3.37 | 2.55 | 2.03 | 3.01 |
| | | 3 | 3.19 | 2.68 | 3.58 | 2.83 | 2.22 | 3.37 |
| | | 4 | 3.07 | 2.59 | 3.46 | 2.76 | 2.10 | 3.42 |
| | | 5 | 3.06 | 2.65 | 3.42 | 2.66 | 2.20 | 3.12 |
| | L | 1 | 3.06 | 2.60 | 3.39 | 2.54 | 2.03 | 2.95 |
| | | 2 | 3.00 | 2.62 | 3.26 | 2.42 | 1.94 | 2.84 |
| | | 3 | 3.05 | 2.57 | 3.44 | 2.53 | 1.98 | 3.04 |
| | | 4 | 2.92 | 2.45 | 3.31 | 2.41 | 1.81 | 3.01 |
| | | 5 | 2.92 | 2.51 | 3.24 | 2.41 | 1.93 | 2.82 |
| SPRING | C | 1 | 3.19 | 2.72 | 3.52 | 2.71 | 2.06 | 3.26 |
| | | 2 | 3.27 | 2.74 | 3.67 | 2.54 | 1.97 | 3.03 |
| | | 3 | 3.16 | 2.69 | 3.47 | 2.69 | 2.12 | 3.13 |
| | | 4 | 3.16 | 2.61 | 3.56 | 2.56 | 2.03 | 2.98 |
| | | 5 | 3.19 | 2.70 | 3.53 | 2.72 | 2.14 | 3.18 |
| | F | 0 | 3.28 | 2.90 | 3.56 | 2.78 | 2.15 | 3.38 |
| | | 1 | 3.26 | 2.75 | 3.65 | 2.79 | 2.11 | 3.39 |
| | | 2 | 3.21 | 2.69 | 3.61 | 2.65 | 2.03 | 3.21 |
| | | 3 | 3.22 | 2.75 | 3.55 | 2.79 | 2.22 | 3.26 |
| | | 4 | 3.10 | 2.59 | 3.48 | 2.71 | 2.10 | 3.24 |
| | | 5 | 3.10 | 2.63 | 3.46 | 2.89 | 2.28 | 3.44 |
| | L | 1 | 3.17 | 2.55 | 3.84 | 2.66 | 2.05 | 3.23 |
| | | 2 | 3.22 | 2.80 | 3.55 | 2.59 | 2.00 | 3.16 |
| | | 3 | 3.20 | 2.74 | 3.50 | 2.75 | 2.13 | 3.26 |
| | | 4 | 3.09 | 2.63 | 3.44 | 2.70 | 2.12 | 3.20 |
| | | 5 | 3.08 | 2.59 | 3.44 | 2.69 | 2.12 | 3.19 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]Grow=growing phase from 9 weeks of age through 54 kg, finish=finishing phase from 54 through 100 kg.

Standard errors ranged from .031 to .037 for feed:gain, .045 to .054 for feed:gain grow, .065 to .074 for feed:gain finish, .044 to .053 for daily intake, .050 to .061 for daily intake grow and .065 to .078 for daily intake finish.

TABLE 11

LEAST-SQUARES MEANS FOR PIG WEIGHTS BY FARROWING GROUP-LINE-GENERATION

| FARROW GROUP[a] | LINE[b] | GENERATION | BIRTH WEIGHT | 21-DAY WEIGHT | 42-DAY WEIGHT |
|---|---|---|---|---|---|
| FALL | C | 1 | 1.60 | 4.92 | 11.64 |
| | | 2 | 1.57 | 4.94 | 9.89 |
| | | 3 | 1.64 | 5.26 | 11.28 |
| | | 4 | 1.57 | 5.04 | 10.21 |
| | | 5 | 1.64 | 5.21 | 9.98 |
| | F | 0 | 1.46 | 4.93 | 10.73 |
| | | 1 | 1.54 | 4.91 | 11.22 |
| | | 2 | 1.50 | 5.08 | 10.18 |
| | | 3 | 1.67 | 5.51 | 10.82 |
| | | 4 | 1.54 | 5.00 | 10.08 |
| | | 5 | 1.53 | 5.29 | 10.24 |
| | L | 1 | 1.62 | 4.91 | 10.89 |
| | | 2 | 1.41 | 4.74 | 9.39 |
| | | 3 | 1.50 | 4.58 | 8.78 |
| | | 4 | 1.45 | 4.90 | 9.40 |
| | | 5 | 1.48 | 5.11 | 9.65 |
| SPRING | C | 1 | 1.53 | 5.14 | 10.71 |
| | | 2 | 1.51 | 5.03 | 10.57 |
| | | 3 | 1.63 | 5.42 | 11.53 |
| | | 4 | 1.68 | 5.57 | 10.74 |
| | | 5 | 1.57 | 5.28 | 10.03 |
| | F | 0 | 1.64 | 5.40 | 11.38 |
| | | 1 | 1.50 | 5.10 | 10.95 |
| | | 2 | 1.53 | 5.30 | 10.90 |
| | | 3 | 1.48 | 5.54 | 11.33 |
| | | 4 | 1.43 | 5.13 | 9.66 |
| | | 5 | 1.50 | 4.84 | 10.45 |
| | L | 1 | 1.51 | 4.91 | 10.38 |
| | | 2 | 1.59 | 5.02 | 10.86 |
| | | 3 | 1.61 | 5.42 | 11.43 |
| | | 4 | 1.59 | 5.32 | 10.32 |
| | | 5 | 1.64 | 5.44 | 10.80 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

Standard errors ranged from .019 to .023 for birth weight, .071 to .090 for 21-day weight and .163 to .203 for 42-day weight.

levels for the final statistical models are presented in appendix Tables 30, 31 and 32, respectively. The three way interaction of line x generation x farrowing group was not significant for all traits; however, the subclass least-squares means were the measurements used to quantify response. The select-line means were deviated from the corresponding C-line mean and regressed on WCSD (Table 13) or generation of selection (Table 15).

Component traits

Response to selection was quantified with generation five point estimates for traits that contribute directly to LTGR and LTFC (Table 12). The regressions of response on WCSD for DG, APBF, FG, and FI are presented in Table 13. The three comparisons of interest were response in each of the select lines (F vs. C and L vs. C) and a direct comparison of the two select lines (F vs. L).

Response in the four component traits differed between F and L. Daily gain and FI were higher in F than in C ($P<.05$) by .05 and .11 kg/d, respectively (Table 12). Corresponding with the generation five estimates were significantly positive across-group regressions for DG ($P<.07$) and FI ($P<.05$). However, generation five differences between F and C not significant for APBF and FG. Also, the corresponding regressions of response for APBF and FG on WCSD were not significant (Table 13). Selection under the restricted intake level had opposite effects on these four traits, as compared to selection under ad libitum intake. Improvements relative to C were significant ($P<.05$) for APBF and FG, but differences were non-significant for DG and FI (Table 12). Likewise, across-farrowing group regressions were significant only for APBF and FI (Table 13).

The result of improved gross efficiency for the present study's standard limited line agrees with findings in the mouse (Hetzel and Nicholas, 1986; McPhee

TABLE 12

GENERATION FIVE LEAST-SQUARES MEANS FOR COMPONENT TRAITS OF LEAN TISSUE GROWTH RATE AND LEAN TISSUE FEED CONVERSION BY LINE

| TRAIT | C[a] | F[a] | L[a] |
|---|---|---|---|
| DAILY GAIN | 0.87[a] | 0.92[b] | 0.86[a] |
| ADJUSTED BACKFAT (cm) | 3.39[a] | 3.42[a] | 3.26[b] |
| FEED:GAIN | 3.07[ab] | 3.08[a] | 3.01[b] |
| DAILY INTAKE | 2.66[a] | 2.77[b] | 2.56[a] |

[a]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

Columns with different subscripts are significantly different ($P<.05$).

Standard errors were .006 for daily gain for all three lines and ranged from .269 to .299 for adjusted backfat, .021 to .023 for feed:gain and .036 to .038 for daily intake.

TABLE 13

REGRESSION OF TRAIT ON CUMULATIVE SELECTION DIFFERENTIAL BY FARROWING GROUP-LINE

| TRAIT | FALL F | SPRING F | ACROSS GROUP[a] F | FALL L | SPRING L | ACROSS GROUP[a] L |
|---|---|---|---|---|---|---|
| DAILY GAIN | -0.03 | 0.27** | .13±.06+ | -0.50* | 0.31+ | -.04±.18 |
| DAILY GAIN GROW | 0.04 | 0.19* | .11±.05+ | -0.39 | 0.02 | -.16±.18 |
| DAILY GAIN FINISH | -0.07 | 0.34** | .14±.08 | -0.56+ | 0.45+ | .01±.23 |
| ADJUSTED BACKFAT (cm) | 0.70* | -0.69* | -.01±.30 | -0.25 | -2.48* | -1.51±.65* |
| DAYS TO 104 KG | 1.48 | -30.40** | -14.86±6.37* | 62.8+ | -63.0* | -8.18±27.86 |
| FEED:GAIN | 0.35+ | -0.33+ | .00±.16 | -0.43 | -0.62 | -.54±.24* |
| FEED:GAIN GROW | 0.04 | -0.17 | -.07±.13 | -1.09 | 0.08 | -.43±.57 |
| FEED:GAIN FINISH | 0.71* | -0.37 | .16±.24 | 0.15 | -1.73 | -.91±.75 |
| DAILY INTAKE | 0.25+ | 0.48** | .37±.09** | -1.94* | 0.46 | -.59±.62 |
| DAILY INTAKE GROW | 0.32 | 0.36+ | .34±.13* | -2.03* | 0.19 | -.78±.55 |
| DAILY INTAKE FINISH | 0.15 | 0.75* | .46±.19* | -2.10* | -0.84 | -.44±.68 |
| BIRTH WEIGHT | -0.14 | -0.50 | -.23±.21 | -1.29+ | 0.00 | -.56±.42 |
| 21-DAY WEIGHT | 0.25 | -1.55+ | -.67±.58 | -1.36 | 0.79 | -.15±1.35 |
| 42-DAY WEIGHT | 0.71 | -0.84 | -.09±1.28 | -3.90 | 3.21 | .11±4.49 |
| NUMBER BORN | -4.86 | 0.04 | -2.39±2.60 | 0.85 | -5.44 | -2.72±4.01 |
| NUMBER 21 DAYS | -1.53 | -7.73+ | -4.66±2.65 | -0.21 | -15.3+ | -8.77±6.08 |
| TOTAL WEIGHT BIRTH | -8.55 | -5.13 | -6.83±3.27+ | -10.10 | -8.13 | -8.98±7.86 |
| TOTAL WEIGHT 21 DAYS | -6.61 | -56.90* | -31.97±16.93+ | -1.92 | -67.86 | -39.37±28.4 |

[a]Regression across farrowing group.
+Regression tended to be significant ($P < .10$).
*Regression significant ($P < .05$).
**Regression highly significant ($P < .01$).

TABLE 14

STANDARDIZED[a] REGRESSION OF TRAIT ON CUMULATIVE SELECTION DIFFERENTIAL BY LINE

| | LINE | |
|---|---|---|
| CORRELATED TRAIT | F | L |
| DAILY GAIN GROW | .07±.03 | -.10±.11 |
| DAILY GAIN FINISH | .11±.06 | .01±.17 |
| ADJUSTED BACKFAT (cm) | 0±.01 | -.03±.01 |
| DAYS TO 104 KG | -.10±.04 | -.05±.18 |
| FEED:GAIN | 0±.08 | -.28±.12 |
| FEED:GAIN GROW | -.01±.02 | -.07±.09 |
| FEED:GAIN FINISH | .02±.03 | -.11±.09 |
| DAILY INTAKE | .13±.03 | -.21±.22 |
| DAILY INTAKE GROW | .05±.02 | -.11 ±.08 |
| DAILY INTAKE FINISH | .05±.02 | -.05±.07 |
| BIRTH WEIGHT | -.09±.06 | -.16±.12 |
| 21-DAY WEIGHT | -.06±.05 | -.01±.11 |
| 42-DAY WEIGHT | 0±.05 | 0±.16 |
| NUMBER BORN | -.09±.10 | -.10±.15 |
| NUMBER 21 DAYS | -.19±.11 | -.35±.25 |
| TOTAL WEIGHT BIRTH | -.17±.08 | -.23±.20 |
| TOTAL WEIGHT 21 DAYS | -.25±.13 | -.31±.22 |

[a]Standardized by the ratio of phenotypic standard deviation of ad libitum daily gain to the correlated trait.

TABLE 15

REGRESSION OF TRAIT ON GENERATION BY FARROWING GROUP-LINE

| TRAIT | FALL F | SPRING F | ACROSS GROUP[a] F | FALL L | SPRING L | ACROSS GROUP[a] L |
|---|---|---|---|---|---|---|
| DAILY GAIN | -0.002 | 0.017** | .008±.004+ | -0.013* | 0.009 | -.002±.005 |
| DAILY GAIN GROW | 0.002 | 0.012* | .007±.003+ | -0.010 | 0.001 | -.005±.005 |
| DAILY GAIN FINISH | -0.004 | 0.022** | .009±.005 | -0.015+ | 0.013+ | -.001±.006 |
| ADJUSTED BACKFAT (cm) | 0.043* | -0.046* | -.001±.019 | -0.007 | -0.071* | -.039±.019+ |
| DAYS TO 104 KG | 0.101 | -1.953** | -.93±1.40* | 1.64+ | -1.75+ | -.060±.770 |
| FEED:GAIN | 0.022+ | -0.021+ | 0±.019 | -0.012 | -0.018 | -.015±.007* |
| FEED:GAIN GROW | 0.002 | -0.011 | 0±.010 | -0.029 | 0 | -.014±.015 |
| FEED:GAIN FINISH | 0.044* | -0.024 | .010±.015 | 0.004 | -0.046 | -.021±.021 |
| DAILY INTAKE | 0.015+ | 0.030** | .023±.006** | -0.050* | 0.012 | -.019±.017 |
| DAILY INTAKE GROW | 0.019 | 0.023 | .021±.008* | -0.053* | 0.005 | -.024±.015 |
| DAILY INTAKE FINISH | 0.010 | 0.047* | .029±.012+ | -0.054* | 0.024 | -.015±.018 |
| BIRTH WEIGHT | -0.009 | -0.034+ | -.021±.013 | -0.033+ | 0 | -.016±.012 |
| 21-DAY WEIGHT | 0.015 | -0.101+ | -.043±.037 | -0.036 | 0.022 | -.007±.037 |
| 42-DAY WEIGHT | 0.040 | -0.068 | -.014±.081 | -0.111 | 0.092 | -.009±.124 |
| NUMBER BORN | -0.309 | -0.012 | -.160±.160 | 0.002 | -0.167 | -.082±.109 |
| NUMBER 21 DAYS | -0.102 | -0.502+ | -.302±.161 | -0.032 | -0.444+ | -.238±.168 |
| TOTAL WEIGHT BIRTH | -0.546 | -0.346 | -.446±.197+ | -0.307 | -0.238 | -.273±.212 |
| TOTAL WEIGHT 21 DAYS | -0.452 | -3.726* | -2.09±1.02+ | -0.169 | -1.950 | -1.06±.79 |

[a]Regression across farrowing group.
+Regression tended to be significant (P < .10).
*Regression significant (P < .05).
**Regression highly significant (P < .01).

and Trappett, 1987) and in the pig (McPhee et al., 1988). However, ad libitum gain in the same two studies was improved under a limited intake level, constrasted to no response in the present study.

The decrease in ad libitum feed intake was in agreement with one mouse study (McPhee and Trappett, 1987), but differed from another that reported no intake change (Hetzel and Nicholas, 1986). In contrast, a line of pigs selected for increased ham weight under a restricted intake had increased ad libitum intake. These constrasting results may be due to selection for different traits. Selection pressure was likely placed on lean gain efficiency in the present study; however, selection for increased ham weight under a restricted intake probably placed more pressure on lean tissue gain. The favorably response in feed:gain as the result of selection under a standard limited intake is in agreement with the mouse (Hetzel and Nicholas, 1986; McPhee and Trappett, 1987) and pig (McPhee et al., 1988).

Directly comparing F and L, DG and FI were higher ($P<.05$) in F and APBF and FG were more favorable ($P<.05$) in L. The only direct comparisons of selection under the two feeding levels are in lines of mice selected for increased 21 to 42 d wt under either ad libitum or restricted feeding. An ad libitum line was faster growing, more efficient, had a higher daily intake and deposited fat more rapidly compared to a line selected under restricted feeding (McPhee and Trappett, 1987). However, the restricted line was more efficient at depositing food as lean gain.

Selection under the ad libitum and the standard limited intake resulted in heritable variation for component traits of LTGR and LTFC being exploited differently. Response in the worth of traits under the two methods is contingent on economic values and thus will depend on production costs and the value of the carcass. As an example, use the following as economic values; \$1/.25 cm for backfat, \$1.25/ .1 improvement in efficiency and \$2.25/.1 daily gain. If generation five line differences are compared using these values then an L pig is worth about \$.25 more.

The restricted level will become worth more in relative value as more emphasis is placed on efficiency and carcass lean. In other words, selection under a restricted level places more emphasis on the efficiency of lean growth.

Growth and ultrasonic backfat regressions

The regressions of response on WCSD are presented within and across farrowing group in Table 13. Response often differed between the two farrowing groups. However, this discussion will focus on the across farrowing group regressions.

The magnitude of each regression is dependent on the variance of the correlated trait, as compared to DG. The across farrowing group regression coefficients were standardized by the ratio of phenotypic SD of DG to the correlated trait (Table 14). These estimates of co-heritability allowed for a more equitable comparison of response relative to the other traits.

Response to selection for DG under ad libitum intake tended to be significant ($P<.10$). The realized heritability estimate of $.13\pm.06$ (Table 13) was similar to estimates of .20 reported by Rahnefeld and Garnett (1976) and Fredeen and Mikami (1986e) as the result of selection for increased postweaning growth rate. Higher estimates were reported by Woltmann et al. (1992) (.37 and .38) as the result of divergent selection for postweaning growth rate. The greater realized response in this study may be due to the period over which selection occurred or because selection pressure was placed in both an upward and downward direction. Similar realized heritabilities were also reported as the result of selection for increased weight at 200 d by Kuhlers and Jungst (1991a) (.18) and Kuhlers and Jungst (1991b) (.26) in a Duroc and Landrace line, respectively.

In L, a non-significant response for growth of -.04 was seen (Table 13). This is not a measure of realized heritability, rather a correlated measure, because the nutritional environment under which L boars were selected differed from the ad libitum environment under which response was measured in barrows and gilts. A negative estimate of response is possible since direct response was not measured. However, measurement of response to selection for growth was of secondary interest and line comparisons of component traits for LTFC and LTGR were of primary interest. The correlated responses of pigs fed under ad libitum intake and selected under a method of limit feeding is also of practical significance, since market barrows and gilts are not commonly limit fed in the U.S. swine industry.

Falconer (1952) expressed the interaction of two nutritional environments as a genetic correlation between two distinct traits. Thus the directional change in ad libitum fed L pigs was dependent on the genetic correlation between gain under ad libitum and restricted intake levels. The only justification for selection under an environment different from that in which the animal is expected to perform would be an increased heritability in the parental environment (Falconer, 1952). Heritability must compensate upward as the genetic correlation between two traits or environments weakens. Weak to moderate realized genetic correlations of .28 (Hetzel and Nicholas, 1986) and .54 (McPhee and Trappett, 1987) resulting from selection under ad libitum and a standardized level of intake were reported in mice. Fowler and Ensminger (1960) reported a stronger realized genetic correlation of .70 between a line of pigs selected under ad libitum intake and one selected under 70% of ad libitum.

Direct response under the same nutritional environment under which selection occurred could only be estimated for L using boar data. The regression of generation mean on WCSD resulted in realized heritability estimates of .29 and .16 for SFG and FFG, respectively. These are comparable to realized heritability estimates of .19 (Hetzel and Nicholas, 1986) and .33 (McPhee and Trappett, 1987) reported in lines of mice selected under restricted intake. McPhee et al., (1988) reported a realized heritability of .43 in a line of pigs, as the result of selecting for increased ham weight under restricted feeding. Progress per generation was estimated to be .017 and .008 for the SFG and FFG, respectively. Caution should be taken since the estimates from the present study were derived with no limit-fed control and the generation means were from only 36 boars within each farrowing group.

In the SFG, a majority of the F and L response in DG was the result of a correlated increase in DG2 (Table 13). Growth rate from 154 to 200 days accounted for much of the increase in 200-d weight (Kuhlers and Jungst, 1991a). This correlated response may be related to the difference between weight ranges in which boars were selected and response was measured. Boars from both lines were selected over a weight range of 36 to 104 kg. Response was measured in the barrows and gilts from 9 wk of age (approximately 20 kg) through 100 kg. Boars were not selected over the weight range that included the first half of DG1 which may explain the smaller amount of response during the growing period.

Correlated changes in D104 mirrored DG response in both lines and farrowing groups (Tables 9, 13 and 14). A co-heritability (Table 14) nearly as high for D104 as the realized heritability in F (-.10 versus .13) indicates that selection for D104 would have been nearly as effective in changing DG as direct selection.

Response in APBF of the F line was significant , but opposite in direction in FFG and SFG (Tables 13 and 15). This resulted in an across farrowing group co-heritability of 0 (Table 14). In L, a significant decrease in APBF was seen in the across farrowing group regression. A line of pigs selected for increased growth rate became less fat relative to controls, but a line selected for decreased fat did not improve in growth rate (Fredeen and Mikami, 1986e). Duroc and Landrace lines selected for increased 200-d weight each increased in backfat thickness at a constant age of 200 d (Kuhlers and Jungst, 1991ab). However, when backfat was adjusted to a constant weight this difference was removed. Woltmann (1989) reported a line selected for increased growth had 15.8% more backfat than a line selected for decreased growth when both were allowed ad libitum intake, but backfat was similar when both lines were limited to the same level of intake. Because of the lack of a control line it is impossible to determine what proportion of the fat differences under ad libitum intake is due to upward versus downward selection for gain.

The correlated fat decrease in L agrees with other studies in both mice and pigs. A line selected for increased ham weight under a limited intake grew faster and was leaner when fed either ad libitum or the intake level under which selection took place (McPhee et al., 1988). Improvements in carcass fat or rate of fat deposition were the result of selecting mice under a limited nutritional environment. The ratio of protein to fat was higher, compared to a line selected under ad libitum intake, when fed either ad libitum or the restricted level under which selection took place (McPhee and Trappett, 1987) and the rate of fat deposition was lowest in the line selected under a limited intake when fed either intake level (Hetzel and Nicholas, 1986).

A four-way interaction was significant for APBF ($P<.05$) (Table 16). In the SFG, gilts in all three lines were consistently .25 to .30 cm leaner than barrows. The cause of the interaction may be how the sex-line combinations performed within each farrowing group. The sex difference was consistently larger in L, than either C or F. If this is a true difference, predication of carcass lean content using barrow data would underestimate lean in L gilts relative to C and F.

Intake and feed efficiency regressions

Pen feed consumption and efficiency are presented in Table 10. In F,

TABLE 16

MEANS FOR BACKFAT THICKNESS BY FARROWING GROUP-LINE-GENERATION-SEX

| FARROW GROUP[a] | LINE[b] | GENERATION | ADJUSTED BACKFAT BY SEX BARROWS | GILTS |
|---|---|---|---|---|
| FALL | C | 1 | 3.23 | 3.08 |
| | | 2 | 3.33 | 3.17 |
| | | 3 | 3.00 | 2.98 |
| | | 4 | 3.07 | 2.83 |
| | | 5 | 3.07 | 2.98 |
| | F | 1 | 3.07 | 3.06 |
| | | 2 | 3.42 | 3.28 |
| | | 3 | 3.16 | 2.97 |
| | | 4 | 3.24 | 2.97 |
| | | 5 | 3.31 | 3.15 |
| | L | 1 | 3.13 | 3.09 |
| | | 2 | 3.42 | 3.14 |
| | | 3 | 3.18 | 2.77 |
| | | 4 | 2.97 | 2.58 |
| | | 5 | 3.29 | 2.90 |
| SPRING | C | 1 | 3.56 | 3.41 |
| | | 2 | 3.61 | 3.39 |
| | | 3 | 3.62 | 3.30 |
| | | 4 | 3.70 | 3.43 |
| | | 5 | 3.89 | 3.59 |
| | F | 1 | 3.72 | 3.54 |
| | | 2 | 3.53 | 3.24 |
| | | 3 | 3.38 | 3.19 |
| | | 4 | 3.54 | 3.35 |
| | | 5 | 3.71 | 3.48 |
| | L | 1 | 3.71 | 3.42 |
| | | 2 | 3.31 | 3.24 |
| | | 3 | 3.37 | 3.18 |
| | | 4 | 3.43 | 3.16 |
| | | 5 | 3.61 | 3.32 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.
[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

correlated response in efficiency and intake differed across farrowing groups. The net result was no response in feed:gain and a significant increase (P<.01) in daily intake (Tables 13 and 15). The lack of improvement in efficiency was the result of gain and intake responding upward at the same relative magnitude. This can be seen in the standardized regression of FI on WCSD (Table 14). A co-heritability nearly as large for FI as DG indicates selection for FI would change DG nearly as rapidly as direct selection. Small improvements in efficiency were also reported by Rahnefeld (1973) where after eight generations of selection for gain under ad libitum intake a smaller than predicted improvement of .04 kg/kg gain was realized.

The strong relationship between DG and FI would suggest intake to be the major correlated trait when selecting for increased growth under ad libitum intake. In summarizing the literature, the genetic correlation between gain and intake was about .90 (Wyllie et al., 1979; Standal and Vangen, 1985). In agreement with this correlation are the findings of Woltmann et al. (1992), who concluded that changes in feed intake explained much of the direct response to selection for post-weaning gain. The same study concluded that much of the intake increases were utilized for the deposition of fat. This would indicate that the relationship between intake and lean growth rate is weak in comparison to that between intake and gross growth rate. Kreiter and Kalm (1986) reported a genetic correlation between intake and lean gain of .40 and an unfavorable genetic correlation of .50 between intake and backfat.

A non-significant decrease in intake and a significant improvement in efficiency were the result of selection under a standard restricted intake (Tables 13 and 15). Correlated changes in ad libitum intake, as the result of selection under a restricted intake, varied between studies. A point estimate of ad libitum intake in the mouse was in agreement with the negative regression in the present study (McPhee and Trappett, 1987). However, ad libitum intake point estimates differed from the current study in the mouse (Hetzel and Nicholas, 1986) (no change) and in the pig (McPhee et al., 1988) (increase). All three of the above-mentioned studies were in agreement with the present results for feed:gain, reporting favorable response.

The nutritional environment under which selection took place in L removed much of the variation in daily food consumption. Because of this decrease in variation, selection under a standardized level of intake results in a high correlation between gain and efficiency. Thus it is expected that improvements in efficiency should be of similar magnitude as those in gain. Feeding L progeny under ad libitum intake resulted in the expected improvement in efficiency; however, there was increase in gain. Direct selection for improved feed efficiency has been relatively unsuccessful (Bernard and Fahmy, 1970; Jungst et al., 1981; Webb and King, 1983). Selection for efficiency was under an ad libitum nutritional environment in each of these studies. Based on the present study, selection for feed efficiency was more successful under an environment in which intake variation was removed or greatly decreased.

Response in ad libitum DG and FI were also closely associated (Tables 13 and 15). The expectation of selection under a standard intake would be to increase growth without changing the genetic potential for intake, thus improving overall efficiency. Results from the SFG tend to agree with this hypothesis. This farrowing group exhibited a slight upward trend for intake and improvements in gain and efficiency. However, there were significant decreases for both DG and FI in the FFG.

Most swine studies in which single-trait selection for growth was practiced, did not include correlated changes in feed intake. However, many index selection studies have reported intake results. A significant intake increase was reported in a line selected for decreased backfat and increased gain (Vangen et al., 1980). Overall improvement in an index that includes efficiency, gain and backfat was the result of decreases in intake (McPhee, 1981; Smith et al., 1991). Improvements were realized for backfat and efficiency, but growth rate was unchanged. Genetic potential for intake will be important for the long-range improvement of pigs and a number of authors have discussed the importance of appetite as it applies to genetic improvement in the pig (Fowler, 1986; Kreiter and Kalm, 1986; Vangen and Kolstad, 1986; Brandt, 1987; Kanis, 1991b).

Pig weights and reproductive performance

Individual pigs weights at birth, 21 and 42 d are presented in Table 11. All three weights are considered traits of the pig, even though they are heavily influenced by the maternal environment. There was a tendency for the regressions of all three weights to be negative; however, none of the regressions were significant (Tables 13 and 15). In general, the literature suggests that early pigs weights are relatively unaffected by selection for increased growth. Weight at 42 d was unchanged as the result of selection for gain (Rahnefeld, 1973). Weights at birth and 21 d decreased as the result of selection for increased 200-d weight (Kuhlers and Jungst, 1991b), but the regressions of correlated response on selection were non-significant. Co-heritabilities for weights at birth, 21 and 35 d were 0, as the result of selection for increased 70-d weight (Kuhlers and Jungst, 1990).

Pig weights at young ages are influenced to a large extent by the number of pigs in a litter and the ability of the sow to care for that number of pigs. Litters were not standardized throughout the present study, thus pig weights, litter weights and number of pigs were partially confounded. Within a particular line, large amounts of variation existed between generations for litter weights and number of pigs at birth, 21 and 42 d of age. The three way interaction of line x farrowing group x generation was not significant for NB, N21D, N42D, LWB, LW21D or LW42D (Table 17). The line x farrowing group interaction was significant for N21D, N42D, LW21D and LW42D (Table 33) and the interaction means are presented in Table 18. The interaction was the result of the select lines outperforming C in the FFG, but C was superior to the select lines in the SFG.

The NB, N21D, LWB and LW21D regressions were negative for both lines; however, the only tendencies for significance (P<.10) were in F. The regressions of LWB and LW21D on WCSD and N21D and LW21D on generation all tended to be significant in F (Tables 13 and 15). Reproductive performance was only measured on gilts, thus measures of lifetime performance and longevity were not available. Fredeen and Mikami (1986c) concluded that reproductive performance was enhanced by selection for an index of gain and backfat, based on their findings and those reported in the literature. However, when either trait was selected for individually reproductive performance was not affected. Cleveland et al. (1988) reported non-significant correlated changes for litter traits as the result of selection for an index of gain and backfat. Selection for lean growth rate and percent lean adversely affected litter size at birth and 21 d (DeNise et al., 1983). Litter size at 21 d in second parity females was nearly two pigs less in the select lines. Correlated response in reproductive traits, resulting from selection under a restricted intake level, has not been reported in the pig.

First and second service conception rate was measured during generations 2 through 4. Generation number was relative to the amount of selection that had taken place in the female. Line means for conception rate were non-significant (Table 19 and 36). Conception rate and farrowing rate were not affected when selection was for total carcass lean or percent lean (DeNise et al., 1983). In the presnt study, additional measurements of female breeding performance were not available due to management. Gilts were only bred during certain time periods in

TABLE 17

MEANS FOR NUMBER OF PIGS AND TOTAL LITTER WEIGHT AT BIRTH, 21 AND 42 DAYS BY FARROWING GROUP-LINE-GENERATION

| FARROW GROUP[a] | LINE[b] | GENERATION[c] | NUMBER BORN | NUMBER 21 DAYS | NUMBER 42 DAYS | TOTAL WEIGHT BIRTH | TOTAL WEIGHT 21 DAYS | TOTAL WEIGHT 42 DAYS |
|---|---|---|---|---|---|---|---|---|
| FALL | C | 0 | 8.61 | 6.77 | 6.65 | 13.8 | 33.2 | 77.3 |
| | | 1 | 10.18 | 8.05 | 7.55 | 16.0 | 39.7 | 74.6 |
| | | 2 | 9.61 | 7.68 | 7.36 | 15.8 | 40.4 | 82.9 |
| | | 3 | 9.12 | 7.12 | 6.77 | 14.3 | 35.8 | 69.0 |
| | | 4 | 10.04 | 7.32 | 7.12 | 16.5 | 37.9 | 70.9 |
| | F | 0 | 9.78 | 8.26 | 8.11 | 15.1 | 40.6 | 90.9 |
| | | 1 | 9.82 | 8.14 | 7.64 | 14.8 | 41.6 | 78.1 |
| | | 2 | 9.74 | 8.30 | 8.26 | 16.3 | 45.8 | 89.4 |
| | | 3 | 9.15 | 7.96 | 7.70 | 14.1 | 39.8 | 77.5 |
| | | 4 | 9.46 | 7.92 | 7.73 | 14.5 | 41.9 | 79.1 |
| | L | 0 | 9.35 | 8.04 | 7.85 | 15.1 | 39.4 | 85.4 |
| | | 1 | 9.67 | 7.75 | 7.46 | 13.6 | 36.7 | 70.0 |
| | | 2 | 9.96 | 8.77 | 8.56 | 14.9 | 40.2 | 75.2 |
| | | 3 | 9.52 | 8.00 | 7.87 | 13.8 | 39.2 | 74.0 |
| | | 4 | 10.32 | 7.84 | 7.60 | 15.3 | 40.1 | 73.4 |
| SPRING | C | 0 | 9.04 | 7.75 | 7.58 | 13.8 | 39.8 | 81.2 |
| | | 1 | 9.20 | 7.68 | 7.56 | 13.9 | 38.6 | 79.9 |
| | | 2 | 8.74 | 7.81 | 7.63 | 14.3 | 42.3 | 87.9 |
| | | 3 | 9.04 | 8.12 | 8.00 | 15.2 | 45.2 | 85.9 |
| | | 4 | 10.19 | 9.04 | 8.73 | 16.1 | 47.7 | 87.6 |
| | F | 0 | 8.96 | 7.84 | 7.68 | 13.4 | 40.0 | 84.1 |
| | | 1 | 9.25 | 7.55 | 7.40 | 14.2 | 40.0 | 80.7 |
| | | 2 | 9.81 | 8.23 | 8.00 | 14.5 | 45.6 | 90.8 |
| | | 3 | 10.11 | 7.69 | 7.65 | 14.4 | 39.4 | 73.9 |
| | | 4 | 9.54 | 6.77 | 5.53 | 14.4 | 32.8 | 57.9 |
| | L | 0 | 9.65 | 8.00 | 7.87 | 14.6 | 39.2 | 81.8 |
| | | 1 | 9.14 | 7.43 | 7.29 | 14.5 | 37.2 | 78.9 |
| | | 2 | 8.64 | 7.44 | 7.36 | 13.9 | 40.3 | 84.0 |
| | | 3 | 9.62 | 8.16 | 8.00 | 15.3 | 43.4 | 82.6 |
| | | 4 | 9.65 | 6.92 | 6.81 | 15.8 | 37.7 | 73.6 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]Generation represents the amount of selection that occurred in the sow.

Standard errors ranged from .288 to .536 for number born, .266 to .608 for number 21 days, .248 to .592 for number 42 days, .508 to .911 for total weight birth, 1.239 to 3.099 for total weight 21 days and 3.007 to 6.478 for total weight 42 days.

TABLE 18

LEAST-SQUARES MEANS FOR NUMBER OF PIGS AND TOTAL LITTER WEIGHT AT 21 AND 42 DAYS BY FARROWING GROUP-LINE

| FARROW GROUP[a] | LINE[b] | NUMBER 21 DAYS | NUMBER 42 DAYS | TOTAL WEIGHT 21 DAYS | TOTAL WEIGHT 42 DAYS |
|---|---|---|---|---|---|
| FALL | C | 7.38 | 7.09 | 37.5 | 75.3 |
| | F | 8.11 | 7.89 | 41.8 | 82.9 |
| | L | 8.09 | 7.87 | 38.9 | 75.3 |
| SPRING | C | 8.08 | 7.90 | 42.6 | 84.2 |
| | F | 7.62 | 7.25 | 39.6 | 77.5 |
| | L | 7.52 | 7.46 | 39.2 | 79.9 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.
[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.
Standard errors ranged from .192 to .203 for number 21 days, .190 to .201 for number 42 days, 1.01 to 1.07 for total weight 21 days and 2.07 to 2.19 for total weight 42 days.

TABLE 19

LEAST-SQUARES MEANS FOR FIRST AND SECOND SERVICE CONCEPTION RATE BY LINE AVERAGED OVER GENERATIONS[a] TWO, THREE AND FOUR

| LINE[b] | N | FIRST SERVICE CONCEPTION RATE | SECOND SERVICE CONCEPTION RATE |
|---|---|---|---|
| C | 189 | 76.1 | 83.1 |
| F | 190 | 73.2 | 83.2 |
| L | 192 | 76.2 | 81.4 |

[a]Generation represents the amount of selection that occurred in the female.
[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.
Standard errors ranged from .031 to .032 for first service conception rate and was .028 for second service conception rate for all three lines.

order to fill the farrowing room, thus all potentially cyclic gilts were not observed.

Carcass

Carcass data were only collected in generations 3 through 5, thus regressions were not calculated for carcass traits. Means for selected carcass traits are presented in Table 20. The DG that is presented is the average for those barrows that were randomly selected for carcass data collection. The growth of the barrows sampled was very near the average their contemporaries (Table 9). The slight advantage in growth of the carcass barrows was representative of the sex difference for daily gain. Carcass and ultrasonically probed backfat means ranked the same within each line (Table 20), indicating the ultrasonic measurements of backfat gave an accurate assessment of line rankings.

Line differences or time trends were not readily evident across generation (Table 20) and the interaction of line x generation x farrowing group was not significant for any of the carcass traits examined (appendix Table 35), thus they were averaged across generation (Table 21). The line x farrowing group interaction was significant (P<.01) for all carcass traits examined, except MSCORE (P<.07, Table 35). Within farrowing group contrasts were examined for carcass traits (Table 22). In the SFG, select-line barrows were leaner than C barrows (P<.01), but fat differences were not significant in the FFG. Similar responses in the FFG were found for LEA, PLEAN and CUT. Both select lines had smaller loin eyes, decreased percent lean and a lowered cutability (P<.01), compared to C. A line selected for increased 200-d weight had 1.5% less estimated percent lean cuts at generation four (Jungst and Kuhlers, 1987), but a line selected for gain had a 1.5% higher carcass lean after nine generations of selection. Selection under a restricted intake resulted in decreased backfat in ad libitum-fed progeny (McPhee et al., 1988).

TABLE 20

MEANS FOR SELECTED CARCASS TRAITS FROM BARROWS BY FARROWING GROUP-LINE-GENERATION

| FARROW GROUP[a] | LINE[b] | GENER-ATION | DAILY GAIN[c] | PROBED BACKFAT[d] (cm) | CARCASS BACKFAT[d] (cm) | LOIN EYE AREA[d] ($cm^2$) | PERCENT LEAN[e] | LEAN GAIN PER DAY ON TEST[f] |
|---|---|---|---|---|---|---|---|---|
| FALL | C | 3 | 0.87 | 3.05 | 2.98 | 33.6 | 53.5 | 0.349 |
| | | 4 | 0.92 | 3.09 | 3.26 | 31.7 | 51.2 | 0.354 |
| | | 5 | 0.91 | 3.06 | 3.06 | 31.2 | 51.9 | 0.356 |
| | F | 3 | 0.89 | 3.29 | 3.30 | 30.1 | 51.2 | 0.343 |
| | | 4 | 0.93 | 3.29 | 3.36 | 28.7 | 49.9 | 0.348 |
| | | 5 | 0.90 | 3.30 | 3.22 | 27.6 | 49.7 | 0.333 |
| | L | 3 | 0.84 | 3.31 | 3.21 | 30.9 | 51.0 | 0.321 |
| | | 4 | 0.86 | 2.87 | 3.16 | 29.2 | 51.3 | 0.324 |
| | | 5 | 0.87 | 3.33 | 3.25 | 28.2 | 49.7 | 0.327 |
| SPRING | C | 3 | 0.88 | 3.72 | 3.80 | 26.1 | 46.3 | 0.285 |
| | | 4 | 0.82 | 3.72 | 3.85 | 28.5 | 47.2 | 0.300 |
| | | 5 | 0.89 | 3.94 | 4.04 | 25.9 | 46.3 | 0.303 |
| | F | 3 | 0.91 | 3.48 | 3.26 | 27.5 | 48.4 | 0.310 |
| | | 4 | 0.92 | 3.35 | 3.48 | 29.0 | 48.8 | 0.343 |
| | | 5 | 0.96 | 3.73 | 3.76 | 24.9 | 46.2 | 0.318 |
| | L | 3 | 0.89 | 3.29 | 3.20 | 28.9 | 48.9 | 0.307 |
| | | 4 | 0.87 | 3.42 | 3.51 | 28.1 | 47.8 | 0.321 |
| | | 5 | 0.90 | 3.65 | 3.59 | 25.0 | 46.8 | 0.307 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]Average daily gain of the barrows that were slaughtered.

[d]Adjusted to 104 kg.

[e]Predicted percentage lean contained in the carcass.

[f]Predicted lean gain per day while on test from 9 weeks of age through 100 kg.

Standard errors ranged from .012 to .024 for daily gain, .075 to .144 for probed backfat, .065 to .142 for carcass backfat, .606 to 1.053 for loin eye area, .418 to .765 for percent lean and .005 to .009 for lean gain per day on test.

TABLE 21

LEAST-SQUARES MEANS FOR CARCASS TRAITS FROM BARROWS BY FARROWING GROUP-LINE

| TRAIT | FARROWING GROUP-LINE[a] | | | | | |
|---|---|---|---|---|---|---|
| | FALL C | FALL F | FALL L | SPRING C | SPRING F | SPRING L |
| DAILY GAIN[bc] | 0.90 | 0.90 | 0.86 | 0.87 | 0.93 | 0.89 |
| PROBED BACKFAT (cm)[cd] | 3.07 | 3.30 | 3.19 | 3.79 | 3.52 | 3.45 |
| CARCASS BACKFAT (cm)[d] | 3.10 | 3.30 | 3.21 | 3.89 | 3.50 | 3.44 |
| LOIN EYE AREA ($cm^2$)[cd] | 32.2 | 28.8 | 29.4 | 26.9 | 27.1 | 27.4 |
| PERCENT LEAN[e] | 52.2 | 50.3 | 50.6 | 46.6 | 47.8 | 47.9 |
| LEAN GAIN PER DAY ON TEST[cf] | 0.353 | 0.341 | 0.324 | 0.296 | 0.323 | 0.312 |
| CARCASS GRADE[g] | 2.01 | 2.35 | 2.19 | 3.35 | 2.87 | 2.97 |
| CUTABILITY[h] | 57.6 | 55.1 | 55.7 | 53.2 | 54.3 | 54.5 |
| LENGTH (cm) | 77.9 | 77.3 | 77.7 | 78.3 | 79.6 | 79.1 |
| MARBLING SCORE[i] | 3.45 | 3.49 | 3.18 | 3.07 | 3.43 | 3.30 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.; C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake. Interaction significant ($P<.05$) for all traits, except for marbling score where $P=.06$. See Table 22 for within farrowing group contrasts of line.

[b]Average daily gain of the barrows that were slaughtered.

[c]Line significant ($P<.05$).

[d]Adjusted to 104 kg.

[e]Predicted percentage lean contained in the carcass.

[f]Predicted lean gain per day while on test from 9 weeks through 100 kg.

[g]Carcass grade = (4 x 10th backfat) - muscle score, where 1=thick, 2=average, 3=thin.

[h]Cutability is the 4 major wholesale cuts (ham, loin, boston butt, picnic) expressed as a percentage of the chilled carcass weight.

[i]Loin eye marbling: 1=traces, 2=slight, 3=small, 4=moderate, 5=abundant.

Standard errors ranged from .009 to .010 for daily gain, .053 to .061 for probed backfat, .058 to .067 for carcass backfat, .495 to .570 for loin eye area, .353 to .409 for percent lean, .0038 to .0044 for lean gain per day on test, .121 to .140 for carcass grade, .361 to .416 for cutability, .246 to .285 for length and .103 to .121 for marbling score.

TABLE 22

WITHIN FARROWING GROUP-LINE CONTRASTS FOR CARCASS TRAITS, TESTICULAR VOLUME AT 5 MONTHS AND FRONT-END STRUCTURE

| | CONTRAST[a] | | | | | |
|---|---|---|---|---|---|---|
| TRAIT | FALL C vs F[b] | FALL C vs L | FALL F vs L | SPRING C vs F | SPRING C vs L | SPRING F vs L |
| VOLUME AT 5 MONTH | -55.51** | 63.10** | 118.61** | -30.90 | 1.14 | 32.04 |
| STRUCTURE | 0.06 | -0.22 | -0.28+ | 0.37** | 0.19 | -0.18 |
| CARCASS BACKFAT (cm)[c] | -0.20 | -0.11 | -0.09 | 0.39** | 0.46** | 0.07 |
| LOIN EYE AREA ($cm^2$)[c] | 3.36** | 2.75** | -0.60 | -0.22 | -0.51 | -0.29 |
| PERCENT LEAN[d] | 1.91** | 1.56* | -0.36 | -1.13 | -1.24+ | -0.11 |
| LEAN GAIN PER DAY ON TEST[e] | 0.011 | 0.029** | 0.017* | -0.027** | -0.015* | 0.012 |
| CARCASS GRADE[f] | -0.034 | -0.19 | 0.15 | 0.47+ | 0.37 | -0.10 |
| CUTABILITY[g] | 2.44** | 1.85** | -0.59 | -1.02 | -1.30* | -0.28 |
| LENGTH (cm) | 0.68 | 0.28 | -0.40 | -1.31** | -0.80 | 0.52 |
| MARBLING SCORE[h] | -0.04 | 0.27 | 0.31* | -0.36** | -0.23 | 0.13 |

[a]These are line contrasts (differences) within farrowing group tested using bonferroni t statistics, where + = P<.10, * = P<.05 and ** = P<.01.

[b]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.; C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]Adjusted to 104 kg.

[d]Predicted percentage lean contained in the carcass.

[e]Predicted lean gain per day while on test from 9 weeks through 100 kg.

[f]Carcass grade = (4 x 10th backfat) - muscle score, where 1=thick, 2=average, 3=thin.

[g]Cutability is the 4 major wholesale cuts (ham, loin, boston butt, picnic) expressed as a percentage of the chilled carcass weight.

[h]Loin eye marbling: 1=traces, 2=slight, 3=small, 4=moderate, 5=abundant.

There was a line x farrowing group interaction for LDG (Table 21). In the FFG, both C and F were superior to L (P<.05) for LDG. In the SFG, F and L were significantly higher than C for LDG by 9 and 5%, respectively. Across farrowing group means for LDG were significantly higher in F, as compared to L (P<.05). Selection on a restricted intake level changed the rate of tissue deposition toward protein in the mouse (McPhee and Trappett, 1987). Lean growth responded favorably in a line selected for increased ham weight under a standard limited intake level (McPhee et al., 1988). Response was positive under either ad libitum intake or the level under which selection took place. The authors suggested that response to selection for lean growth may be increased under a restricted level of intake, as compared to the more common ad libitum nutritional environment. Lean growth was also increased when selection was on an index of gain and backfat (Vangen, 1980; Cleveland et al., 1983a) or when selection was for weight of lean cuts (Leymaster et al., 1979).

Efficiency of lean growth was not directly measured, but some general conclusion can be drawn. In the SFG, LDG (Table 22) and FG (Table 13) improved in both select lines, indicating efficiency of lean growth was also improved. Results from the FFG were not as clear. An undesirable increase in the FG of F, coupled with a non-significant change in LDG, indicated the changes in lean growth efficiency were unfavorable. Lean growth was significantly lower for L in the FFG, but FG was improved with selection. Improvements in lean growth efficiency of L would result if the improvement in FG outweighed the decrease in LDG. Averaged across replicates, it appears that lean growth efficiency was improved in L and was unchanged in F.

A number of other studies have reported improvements in lean growth efficiency as the result of selection on an index that combined two or more traits or for gain under a restricted intake. Improvements in lean efficiency were realized when selecting for an index of increased gain and decreased backfat (Cleveland et al., 1983b) and the breeding objective of lean tissue efficiency was improved when selecting on an index of gain, efficiency and backfat when pigs were tested under ad libitum intake (McPhee, 1981; Ellis et al., 1983) or a standard limited intake (McPhee, 1981; Henderson et al., 1983). In both studies improvements in efficiency were greater under ad libitum intake. McPhee and Trappett (1987) concluded selection under a standard restricted intake level in mice is the best nutritional environment if the breeding objective is efficiency of lean growth. A line of pigs selected for increased lean under a limited nutritional environment deposited lean more efficiently when fed either ad libitum or the level at which selection took place (McPhee et al., 1988).

Movement and structure

Movement and front-end structure were evaluated on all fifth generation barrows and gilts upon removal from test. Line rankings for MOVE (C > L > F) were consistent across farrowing groups (Table 23). Within the SFG the ranking of lines for STRU and MOVE was consistent. However, in the FFG line rankings differed. For both STRU and MOVE F ranked last; however, L ranked above C for STRU and C above L for MOVE.

Line means for DG were related more closely with STRU than with MOVE. The interaction of line x farrowing group was significant for both STRU and DG, but not significant for MOVE (Table 37). The DG interaction was the result of L ranking below C and F in the FFG and F ranking above C and L in the SFG (Table 23). The significant interaction for STRU indicated an inverse relationship between DG and STRU. Woltmann et al. (1987) reported a similar interaction. A fast growth line was superior in structure in the SFG and a slow growth line superior in

TABLE 23

LEAST-SQUARES MEANS FOR MOVEMENT AND STRUCTURAL SOUNDNESS AT OFF TEST IN GENERATION FIVE BY FARROWING GROUP-LINE

| | FARROWING GROUP-LINE[a] | | | | | |
|---|---|---|---|---|---|---|
| TRAIT | FALL C | FALL F | FALL L | SPRING C | SPRING F | SPRING L |
| DAILY GAIN | 0.89 | 0.89 | 0.84 | 0.87 | 0.95 | 0.88 |
| MOVEMENT[b] | 5.60 | 5.26 | 5.37 | 5.59 | 5.34 | 5.53 |
| STRUCTURE[c] | 5.32 | 5.26 | 5.53 | 5.54 | 5.17 | 5.34 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.; C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.
[b]Line significant (P<.01).
[c]Farrowing group by line interaction significant (P<.05). See Table 22 for within farrowing group contrasts of line.
Standard errors ranged from .007 to .009 for daily gain, .082 to .111 for movement and .071 to .097 for structure.

TABLE 24

PHENOTYPIC PARTIAL CORRELATIONS BETWEEN MOVEMENT, STRUCTURE, DAILY GAIN AND PROBED BACKFAT

| TRAIT | DAILY GAIN | PROBED BACKFAT | MOVEMENT | STRUCTURE |
|---|---|---|---|---|
| DAILY GAIN | 1.000 | .211 | .138 | .078 |
| PROBED BACKFAT | | 1.000 | .200 | .147 |
| MOVEMENT | | | 1.000 | .753 |
| STRUCTURE | | | | 1.000 |

the FFG.

A low partial phenotypic correlation between STRU and DG indicates a weak relationship between the traits (Table 24). A similar phenotypic correlation between DG and STRU (.13) was reported by Woltmann et al. (1987) in an evaluation of structure in a fast and slow growth line. However, the phenotypic correlation is not necessarily a good indicator of the genetic relationship between DG and STRU. Rothschild et al. (1988) reported no correlated response in ADG, as the result of selection for either increased or decreased structure. The phenotypic correlation between STRU and MOVE in the present study was relatively high (.75) and agrees with a phenotypic correlation of .87 reported by Rothschild and Christian (1988).

Within farrowing group contrasts for structure indicated that L tended to be more sound than F (P<.10) in the FFG and C more sound that F (P<.01) in the SFG (Table 22). The chi-square statistic was used to test for the independence of MOVE or STRU and line (Tables 25, 26 and 27). Movement scores were pooled across farrowing groups because of the lack of interaction. A significant chi-square was the result of a smaller proportion of F barrows and gilts considered sound (Table 25). Due to the significant line x farrowing group interaction, STRU was tested within farrowing group. A significant chi-square in the SFG resulted from a smaller proportion of F considered sound (Table 27). These results were similar to those for MOVE across farrowing groups. The significant test for independence in the FFG was the result of a larger proportion of L considered sound and a smaller percentage considered unsound (Table 26). The results of the chi-square tests using the arbitrary classifications were closely related to the line means for MOVE and STRU, as discussed earlier (Table 23).

TABLE 25

CHI-SQUARE TEST[a] FOR INDEPENDENCE OF MOVEMENT AND LINE IN GENERATION FIVE ACROSS THE FALL AND SPRING FARROWING GROUPS

| | LINE[b] | | | |
|---|---|---|---|---|
| DEGREE OF SOUNDNESS[c] | C | F | L | TOTAL |
| UNSOUND | 59 | 64 | 63 | 186 |
| MODERATELY SOUND | 68 | 73 | 83 | 224 |
| SOUND | 145 | 86 | 113 | 344 |
| TOTAL | 272 | 223 | 259 | 754 |

[a]P=.02 for $X^2_4$

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]A score of less than 5 was considered unsound, a score of 5 or 5.5 was considered moderately sound and a score of 6 or greater was considered sound.

TABLE 26

CHI-SQUARE TEST[a] FOR INDEPENDENCE OF STRUCTURE AND LINE IN GENERATION FIVE OF THE FALL FARROWING GROUP

| | LINE[b] | | | |
|---|---|---|---|---|
| DEGREE OF SOUNDNESS[c] | C | F | L | TOTAL |
| UNSOUND | 28 | 37 | 19 | 84 |
| MODERATELY SOUND | 44 | 50 | 58 | 152 |
| SOUND | 37 | 42 | 59 | 138 |
| TOTAL | 109 | 129 | 136 | 374 |

[a]P=.044 for $X^2_4$

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]A score of less than 5 was considered unsound, a score of 5 or 5.5 was considered moderately sound and a score of 6 or greater was considered sound.

TABLE 27

CHI-SQUARE TEST[a] FOR INDEPENDENCE OF STRUCTURE AND LINE IN GENERATION FIVE OF THE SPRING FARROWING GROUP

| | LINE[b] | | | |
|---|---|---|---|---|
| DEGREE OF SOUNDNESS[c] | C | F | L | TOTAL |
| UNSOUND | 21 | 26 | 24 | 71 |
| MODERATELY SOUND | 66 | 42 | 50 | 158 |
| SOUND | 76 | 26 | 49 | 151 |
| TOTAL | 163 | 94 | 123 | 380 |

[a]P=.013 for $X^2_4$

[b]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[c]A score of less than 5 was considered unsound, a score of 5 or 5.5 was considered moderately sound and a score of 6 or greater was considered sound.

Testicle volume

Testicle volume of generation five boars was measured at two points, 150 d of age and 107 kg (Table 28). There was a line x farrowing group interaction (P<.05) for ADG and TV150 (Table 38). Lines means for these two traits corresponded closely (Table 29). In the FFG growth rates in C and F were very similar, but L was about 15% lower. In the SFG, C and L were similar for growth rate, but F was about 12% higher. The interaction for TV150 can be described very similarly. Within farrowing group contrasts indicate no significant differences in the SFG (Table 22). In the FFG, the line ranking was F > C > L and all contrasts were significant. Mean weight differed between lines at five months of age, mainly due to the differences in daily gain. Line differences for testicle volume were not significant when boars were measured at a common weight (Table 29). However, volume was numerically larger in the two select lines. The only significant difference for TVOT was that boars in the FFG had a 9% greater testicle volume than boars in the SFG.

Testicle volume was measured at the same two points in generation 0 boars, comparing ad libitum versus limited fed boars independent of selection (Woltmann et al., 1990). The results of above-mentioned and the present study were very similar. Limit feeding decreased TV150, but much of the difference had disappeared when volume was measured at a constant weight. Fall-farrowed boars also had larger testicles at off-test in generation 0, agreeing with fifth generation results in the present study. These data suggest that testicular volume at a constant age is dependent on the growth rate of the line. Differences at 107 kg are more influenced by the season of birth and/or testing than either selection or feeding regime. However, it is difficult to separate correlated response and nutritional effects, since the select lines are confounded with intake level.

TABLE 28

AGE IN DAYS AND WEIGHT AT OFF TEST AT WHICH TESTICLES WERE MEASURED IN GENERATION FIVE

| | LINE[a] | | |
|---|---|---|---|
| TRAIT | C | F | L |
| AGE AT 5 MONTH MEASUREMENT | 150.5 | 149.1 | 151.7 |
| WEIGHT AT OFF TEST MEASUREMENT | 106.6 | 107.3 | 107.5 |

[a]C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

TABLE 29

LEAST-SQUARES MEANS FOR GENERATION FIVE TESTICULAR VOLUME AT 5 MONTHS OF AGE AND AT OFF TEST BY FARROWING GROUP-LINE

| | FARROWING GROUP-LINE[a] | | | | | |
|---|---|---|---|---|---|---|
| TRAIT | FALL C | FALL F | FALL L | SPRING C | SPRING F | SPRING L |
| DAILY GAIN | 0.97 | 1.01 | 0.85 | 0.92 | 1.04 | 0.92 |
| VOLUME AT 5 MONTH ($cm^3$)[b] | 273.2 | 328.8 | 210.1 | 249.7 | 280.6 | 248.6 |
| VOLUME AT OFF TEST ($cm^3$)[c] | 305.3 | 318.4 | 316.4 | 305.3 | 318.4 | 316.4 |

[a]Fall group farrowed from mid-September through October and spring group farrowed from mid-March through April.; C=unselected control, F=selected for rapid growth under ad libitum intake, L=selected for rapid growth under restricted intake.

[b]Farrowing group by line interaction significant (P<.01). See Table 22 for within farrowing group contrasts of line.

[c]Line was averaged over farrowing group because farrowing group by line interaction was non-significant (P>.20). Farrowing group was significant (P<.01), with fall and spring volumes equal to 326.4 and 300.4, respectively.

Standard errors ranged from 11.2 to 12.4 for volume at 5 months and 8.1 to 8.2 for volume at off test.

## Summary

Genetic improvement through selection for specific traits is the only method to make permanent changes in a population. For the swine industry to be successful it is essential that economically important traits continue to be improved. Traits such as growth rate, feed intake, efficiency and carcass composition are components of lean growth rate and lean growth efficiency. Specialized terminal or paternal lines should excel in lean growth and lean growth efficiency. Traditionally the above traits have been improved by selecting for either a single or multiple traits in animals allowed ad libitum feed. The most common method of multi-trait selection is an index that combines two or more traits into a single measurement based on genetic parameters and the relative economic value of each trait. Fowler et al. (1976) proposed an alternative selection method for improving lean growth rate and lean growth efficiency in pigs. Under Fowler's method all pigs are allowed a standard amount of food over a given period. Standardizing intake removes the contribution of feed intake to the variation in growth rate. Fowler et al. (1976) hypothesized that selection for rapid growth under a restricted nutritional environment should favor those animals that are most efficient because they will direct proportionately more metabolizable energy toward the synthesis of protein and less toward fat. Thus, selection for growth under a restricted intake should favor lean growth efficiency because feed intake is a constant.

The hypothesis outlined by Fowler et al. (1976) has been tested in three studies using mice (McPhee et al., 1980; Hetzel and Nicholas, 1986; McPhee and Trappett, 1987) and one study using pigs (McPhee et al., 1988). McPhee et al. (1980) initially tested the hypothesis in mice. Two criticisms of the study by McPhee et al. (1980) are: 1) selection occurred over an age range (5 to 9 weeks) that was beyond the period of rapid lean deposition in the mouse, and 2) a line selected for increased growth under ad libitum feeding conditions was not included. Later studies accounted for these problems by selecting for increased weight gain from 3 to 6 weeks under either ad libitum or a restricted intake (Hetzel and Nicholas, 1986; McPhee and Trappett, 1987). McPhee et al. (1988) tested Fowler's hypothesis in the pig by selecting for increased ham weight under a restricted feeding level. However, a line selected under ad libitum feeding was not included, so a direct comparison of selection under ad libitum and restricted feeding has not been made in the pig.

The objective of my study was to quantify and compare response in component traits of lean growth rate and lean growth efficiency ( growth rate, feed intake, feed:gain and composition) to selection for gain under allowed ad libitum or a standard limited intake. The objective tests the hypothesis that response will differ depending on the allowed intake level under which selection occurs. The design used to test the hypothesis included lines of pigs selected for increased growth under: 1) ad libitum intake and 2) a standard limited intake ( 83% of predicted ad libitum intake). The two select lines will be referred to as the ad libitum line and the standard limited intake line, respectively. Select lines of mice and pigs comparable to the standard limited intake line will be referred to as restricted lines. An unselected control line was also maintained to account for environmental fluctuations. Response in both select lines is relative to the control line unless specified. Selection occurred for five generation only in males. Response to selection was measured on barrows and gilts allowed ad libitum access to feed. So, in the ad libitum line selection and response were both under ad libitum feeding conditions; however, in the standard limited intake line selection occurred under 83% of predicted ad libitum intake and response was measured under ad libitum feeding conditions.

Growth rate results are presented by generation in Figure 2. Generation means in the ad libitum and the standard limited intake lines are presented as numerical differences from the control line. Discussion will be centered on results from generation five. Recall response was measured in both lines on ad libitum fed progeny. Daily gain increased in the ad libitum line, but in the standard limited intake line there was no response in daily gain relative to the control line. The positive response in the ad libitum line is in agreement with all previous reports in pigs (Fredeen and Mikami, 1986e; Kuhlers and Jungst, 1991a; Kuhlers and Jungst, 1991b; Woltmann et al., 1992). In contrast, results of the standard limited intake line differs from previously reported results. Selection in mice (Hetzel and Nicholas, 1986; McPhee and Trappett, 1987) and pigs (McPhee et al., 1988) under a restricted intake resulted in positive response in ad libitum fed progeny. In the mouse study that allowed for a direct comparison of select lines, progeny from the ad libitum intake line grew faster than progeny of the restricted intake line (McPhee and Trappett, 1987). This direct comparison could not be made in the pig.

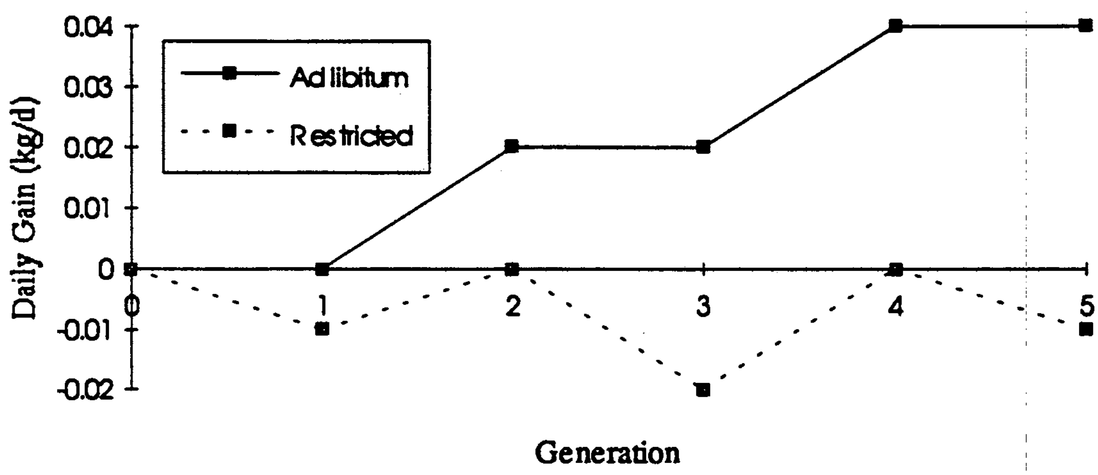


Figure 2. Generation Least-Squares Means for Daily Gain Deviated From the Control Line of Ad Libitum Fed Progeny Sired by Boars From the Ad Libitum or Standard Intake Line

Based on previous reports in mice (Hetzel and Nicholas, 1986; McPhee and Trappett, 1987) and swine (McPhee et al., 1988), it was my expectation that selection for growth under a limited intake would increase growth rate under any nutritional environment. However, selection under the standard limited intake level did not change growth rate in my study. It is possible that species differences in response to selection for growth under a restricted intake exist between mice and pigs. One study in pigs selected for increased ham weight under a restricted intake level, whereas I selected for growth rate in pigs fed a restricted intake. Selection for ham weight under restricted intake probably placed selection pressure on lean growth rate, as opposed to my study that probably placed more selection pressure on lean gain efficiency.

Ad libitum fed progeny did not respond to selection for growth under the standard limited intake. A number of factors may have contributed to this lack of response. First, growth was measured under different environments in the boars fed the standard limited intake level, as compared to the barrows and gilts. Two points contributed to the difference: 1) the allowed feed intake level differed between where selection took place and response was measured (restricted intake in boars vs. ad libitum intake in barrow and gilt progeny), and 2) the range over which growth was measured differed (36 through 104 kg in boars and 9 weeks through 100 kg in barrow and gilt progeny). This indicates that growth rate under the two environments are different traits. Thus, response in the barrow and gilt progeny will depend on the correlation between growth under ad libitum and the standard limited intake. No response in growth in the standard intake line would indicate that the above correlation is zero. Another potential reason for no response in growth is that the recommended daily intake of protein was not met throughout the test period. This was due to the level at which the boars were restricted and the level of protein in the diet. If dietary protein was not sufficient to meet the pig's requirement for maximum growth, especially lean growth, full potential under this standard intake level may not have been expressed. This may have lowered the variation in growth rate and possibly caused error in the selection of boars. Lastly, the initial genetic line that was used to establish the base generation of the ad libitum and standard intake lines was previously selected for increased growth. It is possible that selection limits were being approached and slowed down improvement in growth rate. However, it should be noted that selection limits have not been documented in swine.

Feed intake results are presented by generation in Figure 3. This discussion will be based on generation five deviations from the control. Intake response in my study differed in the two select lines. Ad libitum intake increased in the line selected under ad libitum intake and tended to decrease when selection was under the standard limited intake. The increased daily intake in the ad libitum line is in agreement with a study in pigs (Woltmann et al., 1992) and studies in mice (Hetzel and Nicholas, 1986; McPhee and Trappett, 1987). However, intake results were not as consistent in ad libitum fed progeny out of restricted line parents. A decrease in ad libitum intake in a line of mice selected under a restricted intake was in agreement with my study (McPhee and Trappett, 1987). Contrasting intake results were reported in mice (Hetzel and Nicholas, 1986) (no change) and pigs (increase).

Based on a relatively strong genetic correlation between growth and ad libitum intake (Vangen, 1985) and previous selection results (Hetzel and Nicholas, 1986; McPhee and Trappett, 1987; Woltmann et al., 1992), the increased feed intake in the ad libitum line was expected. It was my expectation that ad libitum feed intake would not change in the standard limited intake line. This expectation is based on the fact that all pigs were selected for growth under a standard intake amount, thus no upward or downward pressure should have been placed on intake. However, intake tended to be lower after five generations of selection in the standard limited intake line. A reason for the unexpected decrease in intake may be the allowed intake difference between the boars (restricted) and the barrow and gilt progeny (ad libitum). Intake under the two environments can be thought of as different traits, much the same as was discussed for growth rate. Intake response in ad libitum fed progeny will depend on the correlation between intake under the two environments. The decrease in ad libitum intake indicates this correlation is negative.

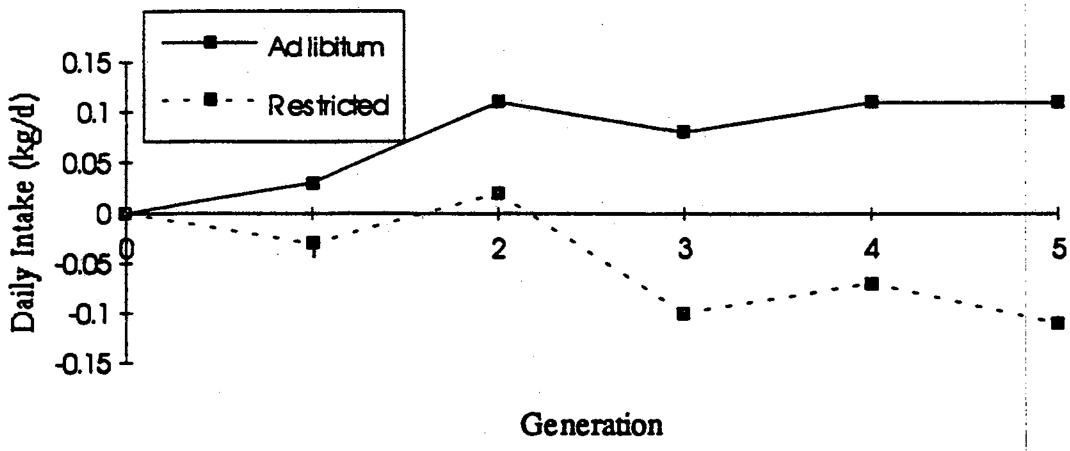


Figure 3. Generation Least-Squares Means for Daily Intake Deviated From the Control Line of Ad Libitum Fed Progeny Sired by Boars From the Ad Libitum or Standard Intake Line

Feed:gain results are presented by generation in Figure 4. This discussion will be based on generation five deviations from the control. In my study feed:gain in the ad libitum line was unaffected by selection, but feed:gain responded favorably ( i.e. decreased) in the line selected under the standard limited intake. Feed:gain in lines of mice selected under ad libitum intake responded favorably (Hetzel and Nicholas, 1986; McPhee and Trappett, 1987), differing from the results of the ad libitum line presented in Figure 4. However, the results from restricted intake lines of mice (Hetzel and Nicholas, 1986; McPhee and Trappett, 1987) and pigs (McPhee et al., 1988) are in agreement with the feed:gain results from the standard limited intake line in my study.

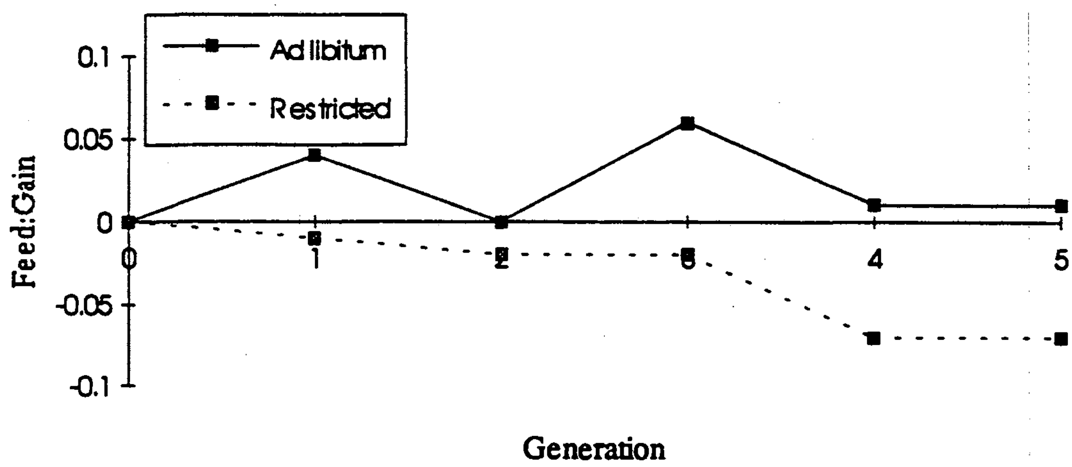


Figure 4. Generation Least-Squares Means for the Feed:Gain Ratio Deviated From the Control Line of Ad Libitum Fed Progeny Sired by Boars From the Ad Libitum or Standard Intake Line

When selection for growth rate is under a standard limited intake, it is expected that feed:gain will improve. If the fastest gaining pigs are selected and feed is held constant, then pigs with the with most desirable (smallest) feed:gain ratio will be selected. Mine and previously reported results (Hetzel and Nicholas, 1986; McPhee and Trappett, 1987; McPhee et al., 1988) agree with this expectation.

Backfat thickness was measured as an indication of the lean composition at test completion. Response in backfat thickness at a constant weight was negative (favorable) in the standard limited intake line and was not different from the control in the ad libitum line. McPhee et al. (1988) also reported decreased backfat as the result of selection for increased ham weight under a restricted intake level. The findings of my study are also similar to results reported in mice. When comparing fat as a percentage of total body weight, it did not change in an ad libitum line and decreased in a restricted line (Hetzel and Nicholas, 1986).

Results of my study agree with the results of selection for an index that included growth rate, feed efficiency and backfat (McPhee, 1981; Henderson et al., 1982). The selection objective of mine and the above two index studies was lean growth efficiency. Selection under the standard limited intake level and the three-trait index (McPhee, 1981; Henderson et al, 1982) resulted in improved feed:gain, decreased backfat, no change in growth rate and a decrease in intake. These studies indicate improvement in the selection objective of lean growth efficiency was be due to a favorable response in gross efficiency and a decrease in backfat. The response in efficiency and backfat came at the expense of decreased intake. Intake is highly correlated with the growth rate. Because growth rate is a trait of major economic importance, selection methods should be designed to increase or at least maintain feed intake. The index and restricted feeding methods that have been designed to select for lean growth efficiency resulted in a deterioration of feed intake, thus alternative methods of selecting for lean growth efficiency should be explored or selection pressure should be placed on other traits.

My study demonstrates that response in the component traits of lean growth rate and the efficiency of lean growth differed depending on the level of intake under which selection occurred. In the ad libitum line, response in ad libitum fed progeny was positive for growth rate and feed intake, but response in feed:gain and backfat was not different from the control line. Favorable response for feed:gain and backfat in ad libitum fed progeny from the standard limited intake line contrasts with the results of the same traits in the ad libitum line. Growth rates did not differ between the standard limited intake and control lines despite a greater daily intake in the latter line. Even though component traits of lean growth rate and lean tissue efficiency were quantified, my study was not designed to allow for the direct measurement of lean growth efficiency and lean growth rate. The next step should be the quantification and comparison of lean growth rate and lean growth efficiency in each of the three lines. The design of the study should include pigs from the three lines in a factorial arrangement of treatments with allowed intake level ( ad libitum intake or the standard limited intake). Individual feed intake and complete carcass separation at test initiation using sibs of tested pigs and at completion will allow for the measurement of lean growth rate and lean growth efficiency.

Direct measurement of lean growth rate and lean growth efficiency should provide a better understanding of the relationship between intake, lean growth rate and lean growth efficiency. Further studies with the ad libitum and the standard limited intake lines will probably be better defined after this more complete quantification of lean growth rate and lean growth efficiency. I have outlined what I feel are some of the potential studies. A better understanding of the relationship between intake, lean gain and lean gain efficiency would provide valuable information for developing swine growth models. In addition, this information could be used in the development of selection indexes that include intake. These indexes should be designed to either maintain or increase intake while improving traits such as growth rate, efficiency and body composition. If the ad libitum and standard limited intake lines are divergent enough for traits such as intake, lean gain and lean gain efficiency when selection is terminated (generation seven) then they may provide a good model for nutritional or physiological studies. Another possibility is that other selection experiments may be suggested. Such studies may include traits other than growth rate when selecting under a restricted feeding level (i.e. select directly for lean growth under restricted feed intake). Recent technological developments in the measurement of body composition in the live pig make direct selection for lean growth rate possible. Problems and criticisms of my selection study should be corrected in any future selection experiments of this type, including more appropriate feeding levels and diets.

This study demonstrates that response in the component traits of lean growth efficiency and lean growth rate differed depending on the intake level under which selection occurred. However, an additional study that directly quantifies lean growth and lean growth efficiency will provide a better understanding of the relationship between lean growth efficiency, lean growth rate and other traits.

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# APPENDIX

# PROBABILITY LEVEL FOR THE FINAL MODELS

TABLE 30

PROBABILITY LEVELS FOR THE INDEPENDENT VARIABLES IN THE MODEL FOR THE GROWTH TRAITS AND PROBED BACKFAT

| INDEPENDENT VARIABLE | DAILY GAIN | DAILY GAIN GROW | DAILY GAIN FINISH | ADJUSTED BACKFAT (cm) | DAYS TO 104 KG |
|---|---|---|---|---|---|
| LINE | .001 | .001 | .001 | .001 | .001 |
| GENERATION (GEN) | .001 | .001 | .001 | .001 | .001 |
| SEX | .001 | .001 | .001 | .001 | .001 |
| FARROWING GROUP (FG) | .123 | .448 | .584 | .001 | .018 |
| DIET(GEN*FG) | .001 | .001 | .001 | .001 | .001 |
| LINE*GEN | .008 | .001 | .001 | .001 | .015 |
| LINE*SEX | .738 | .215 | .666 | .041 | .809 |
| LINE*FG | .001 | .001 | .001 | .001 | .001 |
| LINE*DIET(GEN*FG) | .001 | .001 | .001 | .001 | .001 |
| GEN*SEX | NS | NS | NS | .013 | NS |
| GEN*FG | .001 | .001 | .001 | .001 | .001 |
| SEX*FG | .258 | .417 | .159 | .177 | .545 |
| SEX*DIET(GEN*FG) | .437 | .214 | .091 | NS | .121 |
| LINE*GEN*SEX | NS | NS | NS | .618 | NS |
| LINE*GEN*FG | .001 | .498 | .001 | .001 | .001 |
| LINE*SEX*FG | .010 | .758 | .086 | .005 | .003 |
| GEN*SEX*FG | NS | NS | NS | .258 | NS |
| LINE*GEN*SEX*FG | NS[a] | NS | NS | .033 | NS |

[a]The probability level was >.20 in the full model and thus they were removed from the final (reduced) model. Note that line*diet*sex(gen*fg) was removed from all the final models.

TABLE 31

PROBABILITY LEVELS FOR THE INDEPENDENT VARIABLES IN THE MODEL FOR THE PEN FEED INTAKE AND EFFICIENCY TRAITS

| INDEPENDENT VARIABLE | FEED: GAIN | FEED: GAIN GROW | FEED: GAIN FINISH | DAILY INTAKE | DAILY INTAKE GROW | DAILY INTAKE FINISH |
|---|---|---|---|---|---|---|
| LINE | .001 | .054 | .134 | .001 | .001 | .001 |
| GENERATION (GEN) | .001 | .002 | .004 | .001 | .001 | .001 |
| FARROWING GROUP (FG) | .001 | .001 | .001 | .001 | .009 | .001 |
| DIET(GEN*FG) | .001 | .033 | .003 | .007 | .051 | .012 |
| LINE*GEN | .795 | .119 | .134 | .350 | .196 | .859 |
| LINE*FG | .034 | .375 | .107 | .001 | .004 | .001 |
| LINE*DIET(GEN*FG) | NS[a] | NS | NS | NS | NS | NS |
| GEN*FG | .003 | .201 | .001 | .003 | .690 | .001 |
| LINE*GEN*FG | .067 | .373 | .408 | .026 | .220 | .400 |

[a]The probability level was >.20 in the full model and thus they were removed from the final (reduced) model.

TABLE 32

PROBABILITY LEVELS FOR THE INDEPENDENT VARIABLES IN THE MODEL FOR PIG WEIGHTS AT BIRTH, 21 AND 42 DAYS

| INDEPENDENT VARIABLE | BIRTH WEIGHT | 21-DAY WEIGHT | 42-DAY WEIGHT |
|---|---|---|---|
| LINE | .001 | .001 | .001 |
| GENERATION (GEN) | .001 | .001 | .001 |
| SEX | .001 | .053 | .464 |
| FARROWING GROUP (FG) | .662 | .001 | .001 |
| LINE*GEN | .001 | .001 | .001 |
| LINE*SEX | .463 | .577 | .908 |
| LINE*FG | .001 | .001 | .001 |
| GEN*SEX | .275 | .426 | .807 |
| GEN*FG | .001 | .001 | .001 |
| SEX*FG | .581 | .352 | .279 |
| LINE*GEN*SEX | .814 | .469 | .446 |
| LINE*GEN*FG | .001 | .001 | .001 |
| LINE*SEX*FG | .782 | .204 | .864 |
| GEN*SEX*FGROUP | .109 | .171 | .689 |
| LINE*GEN*SEX*FG | .131 | .162 | .063 |

TABLE 33

PROBABILITY LEVELS FOR THE INDEPENDENT VARIABLES IN THE MODEL FOR THE LITTER WEIGHT AND PIG NUMBER TRAITS

| INDEPENDENT VARIABLE | NUMBER BORN | NUMBER 21 DAYS | NUMBER 42 DAYS | TOTAL BIRTH WEIGHT | TOTAL WEIGHT 21 DAYS | TOTAL WEIGHT 42 DAYS |
|---|---|---|---|---|---|---|
| LINE | .611 | .780 | .691 | .483 | .273 | .431 |
| GENERATION (GEN) | .190 | .587 | .168 | .048 | .031 | .001 |
| FARROWING GROUP (FG) | .145 | .455 | .642 | .143 | .191 | .102 |
| DIET(GEN*FG) | NS | NS | NS | NS | .030 | .015 |
| LINE*GEN | .526 | .225 | .043 | .184 | .040 | .098 |
| LINE*FG | NS | .002 | .001 | NS | .002 | .003 |
| LINE*DIET(GEN*FG) | NS | NS | NS | NS | NS | NS |
| GEN*FG | .237 | NS | .339 | .055 | .417 | .256 |
| LINE*GEN*FG | NS[a] | NS | .177 | NS | .135 | .188 |

[a]The probability level was >.20 in the full model and thus they were removed from the final (reduced) model.

TABLE 34

PROBABILITY LEVELS FOR THE INDEPENDENT VARIABLES IN THE MODEL FOR GENERATION FIVE COMPONENT TRAITS OF LEAN TISSUE GROWTH RATE AND LEAN TISSUE FEED CONVERSION

| INDEPENDENT VARIABLE | DAILY GAIN | ADJUSTED BACKFAT | FEED:GAIN | DAILY INTAKE |
|---|---|---|---|---|
| LINE | .001 | .017 | .065 | .001 |
| SEX | .001 | .001 | .001 | .001 |
| FARROWING GROUP (FG) | .001 | ..001 | - | - |
| DIET(FG) | .001 | .001 | .234 | .015 |
| LINE*SEX | NS[a] | .072 | - | - |
| LINE*FG | .001 | .001 | .015 | .213 |
| LINE*DIET(FG) | .004 | .006 | NS | NS |
| SEX*FG | NS | .321 | - | - |
| SEX*DIET(FG) | NS | NS | - | - |
| LINE*FG*SEX | NS | .063 | - | - |

[a]The probability level was >.20 in the full model and thus they were removed from the final (reduced) model.

TABLE 35

PROBABILITY LEVELS FOR THE INDEPENDENT VARIABLES IN THE MODEL FOR THE CARCASS TRAITS

| INDEPENDENT VARIABLE | DAILY GAIN | PROBED BACKFAT (cm) | CARCASS BACKFAT (cm) | LOIN EYE AREA ($cm^2$) | PERCENT LEAN | LEAN GAIN PER DAY ON TEST | CARCASS GRADE | CUT-ABILITY | LENGTH (cm) | MARBLING SCORE |
|---|---|---|---|---|---|---|---|---|---|---|
| LINE | .002 | .103 | .016 | .008 | .576 | .002 | .746 | .178 | .429 | .092 |
| GENERATION (GEN) | .022 | .002 | .004 | .001 | .001 | .022 | .001 | .174 | .423 | .582 |
| FARROWING GROUP (FG) | .001 | .001 | .001 | .001 | .001 | .001 | .001 | .001 | .001 | .215 |
| DIET(GEN*FG) | NS[a] | NS | NS | NS | NS | NS | NS | NS | NS | .270 |
| LINE*GEN | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| LINE*FG | .001 | .001 | .001 | .001 | .001 | .001 | .005 | .001 | .001 | .062 |
| LINE*DIET(GEN*FG) | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| GEN*FG | NS | .063 | .011 | .024 | NS | NS | .047 | .045 | .003 | .001 |
| LINE*GEN*FG | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |

[a]The probability level was >.20 in the full model and thus they were removed from the final (reduced) model.

TABLE 36

PROBABILITY LEVELS FOR THE INDEPENDENT VARIABLES IN THE MODEL FOR FIRST AND SECOND SERVICE CONCEPTION RATE

| INDEPENDENT VARIABLE | FIRST SERVICE CONCEPTION RATE | SECOND SERVICE CONCEPTION RATE |
|---|---|---|
| LINE | .740 | .874 |
| GENERATION (GEN) | .210 | .197 |
| FARROWING GROUP (FG) | .611 | .797 |
| LINE*GEN | NS[a] | NS |
| LINE*FG | NS | NS |
| GEN*FG | NS | NS |
| LINE*FG*GEN | NS | NS |

[a]The probability level was >.20 in the full model and thus they were removed from the final (reduced) model.

TABLE 37

PROBABILITY LEVELS FOR THE INDEPENDENT VARIABLES IN THE MODEL FOR MOVEMENT AND STRUCURE IN GENERATION FIVE

| INDEPENDENT VARIABLE | MOVEMENT | STRUCTURE | DAILY GAIN |
|---|---|---|---|
| LINE | .010 | .013 | .001 |
| SEX | .140 | .846 | .001 |
| FARROWING GROUP (FG) | .364 | .787 | .001 |
| LINE*SEX | .474 | .020 | .478 |
| LINE*FG | .683 | .031 | .001 |
| SEX*FG | .341 | .847 | .412 |
| LINE*FG*SEX | .119 | .060 | .182 |

[a]The probability level was >.20 in the full model and thus they were removed from the final (reduced) model.

TABLE 38

PROBABILITY LEVELS FOR THE INDEPENDENT VARIABLES IN THE MODEL FOR TESTICULAR VOLUME AT 5 MONTHS AND OFF TEST IN GENERATION FIVE

| INDEPENDENT VARIABLE | DAILY GAIN | TESTICULAR VOLUME AT 5 MONTHS ($cm^3$) | TESTICULAR VOLUME AT OFF TEST ($cm^3$) |
|---|---|---|---|
| LINE | .001 | .001 | .480 |
| FARROWING GROUP (FG) | .208 | .295 | .006 |
| LINE*FG | .002 | .001 | NS[b] |
| COVARIATE[a] | - | .201 | .277 |

[a]The covariate for volume at 5 months of age was age in days and for volume at off test was weight.
[b]The probability level was >.20 in the full model and thus they were removed from the final (reduced) model.

VITA

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