THE UNIVERSITY OF MANITOBA

SELECTION FOR BODY WEIGHT AND FEED EFFICIENCY OF MICE IN THREE NUTRITIONAL ENVIRONMENTS

BY

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A THESIS SUBMITTED TO THE FACULTY
OF GRADUATE STUDIES IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF ANIMAL SCIENCE

WINNIPEG, MANITOBA

1984

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ABSTRACT

Mass selection for adjusted feed efficiency (AFE) and adjusted body weight (ABW) of male mice was practised for seven generations in each of three nutritional environments: corn, rye or wheat. In each environment two control lines, randomly bred, were maintained on either the experimental diet (DC i.e. corn, rye or wheat) or a commercial diet (PC). The three diets were isocaloric (≈16.5 MJ GE/kg) and isonitrogenous (CP ≈13%). Selection was based upon linear adjustment to a common initial body weight for either final weight (ABW) or feed efficiency (AFE) measured between 21 and 35 days of age. Response was determined as a deviation from the appropriate DC line. All animals were placed in specially designed individual cages during the test period.

Half-sib estimates of heritability in the PC line were .13(±.11) for ABW and .19(±.10) for AFE. Half-sib estimates pooled across lines (fed experimental diets) and environments were .24(±.08) for ABW and .20(±.08) for AFE. Realized heritabilities in the ABW lines were: .24(±.06), .06(±.07) and .14(±.06) for the corn, rye and wheat environments respectively. Response to selection for AFE was poor with the highest heritability obtained in the wheat environment ($h^2 = .13 \pm .02$). Mature weights, estimated in generation seven, indicated that selected mice were 3.2 grams heavier than mice from the DC lines. No effects of environment of differences between the ABW and AFE lines for mature weight were significant.

During generation eight, a crossover study was undertaken. Mice from each line (ABW, AFE or DC) in each environment were fed either the corn, rye and wheat diets. Response of adjusted traits was measured as a deviation from the DC line fed the same diet. No significant ($P<.05$) genotype by diet interactions were detected. Mice, however, in the ABW line tended ($P<.18$) to have higher final weights on test (~1 gram) when fed the selection diet compared to the two alternative diets.

With low heritabilities, definitive conclusions are difficult to make. Problems encountered with using mice as a model for growth in practical livestock species are discussed.

Dedicated to my wife, Margaret

ACKNOWLEDGEMENTS

The author is indebted to Dr. W. Guenter for his continued professional and personal support throughout the course of my graduate studies. Sincere appreciation and thanks are extended to Dr. R.J. Parker who permitted a nutritionist to invade his genetics lab. The additional problems and challenges presented to him by having a student involved in an interdisciplinary project were overcome with patience and persistence.

Dr. G.H. Crow provided invaluable statistical advice particularly with regard to computer applications. It should be emphasized, however, that the total responsibility for the validity and interpretation of the analysis used in this study is mine. Dr. Crow's perseverance was admirable and his time was much appreciated. Thanks also to Dr. L.D. Campbell and Dr. P. McVetty who served on the advisory committee.

Sincere thanks are also extended to Mr. Garth Ball who helped with the design and construction of the individual feeder cages. I am grateful to Mrs. Margaret Funk for typing this thesis. Her patience and friendly cooperation, as well as her editing skills, were invaluable.

Personal financial support was provided through post-graduate fellowships, initially, by the Natural Science and Engineering Research Council (NSERC) and, during the last two years, by The Wheat Board of Canada. Their assistance was very much appreciated. Additional project funding was provided by NSERC (Grant #A4438).

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INTRODUCTION

There is growing interest in the potential for using alternative feed sources in animal production, particularly in stimulating the consumption of locally established crops. The burden is traditionally placed on plant breeders who attempt to reduce or eliminate antinutritional components peculiar to a particular grain. Problems arise, however, when the characteristics which make the plant suitable in a specific climate also are responsible for reducing nutrient availability (i.e. rye grain).

Corn is the primary ingredient providing energy in practical poultry rations. Long term selection of birds physiologically adapted to this specific grain tyep might negatively bias nutrient evaluation of alternative feedstuffs. Evidence that commercial broiler chickens are more sensitive to rye grain than other strains or species is abundant (Antoniou, 1980).

Recent research in animal genetics has emphasized the importance of optimizing efficiency of feed utilization in breeding programs rather than just assessing growth rate. The complexities inherent in comparison of feed efficiency measurements during various stages of growth makes careful attention to selection procedure a necessity.

The purpose of this study was to test the relative effectiveness of selection for feed efficiency or body weight in three different nutritional environments (i.e. with mice fed corn, rye or wheat diets). Genotype by diet interactions were tested in a crossover experiment to determine if the relative response to selection on one diet would be specific to that diet. The mouse was deemed a suitable model for this study. Several generations of selection could be completed in a relatively short period and within a limited space. This animal was considered a reasonably typical monogastric species.

LITERATURE REVIEW

I. General

Comprehensive reviews on the outcome of selection for body weight or gain have been published by Malik (1984), McCarthy (1982), Roberts (1981), Roberts (1979), Eisen (1974) and Roberts (1965). Although differences in response were apparent, several simple generalizations can be made.

Selection for body weight or gain is effective, resulting in lines with faster absolute growth rates, larger mature size and increased food consumption (i.e. greater appetites). Heritability (h^2) estimates range from .25 to .40 for post-weaning growth (Eisen, 1976). Falconer (1973), for example, reported realized heritability estimates of .40 for six-week body weight. Sutherland *et al.* (1970) obtained much lower estimates ($h^2 = .22$ to $.29$) for gain between 4 and 11 weeks of age. These were similar to estimates obtained by Hetzel and Nicholas (1982) for gain from three to six weeks of age ($h^2 = .29$).

Gross efficiency (gain/feed) is higher in large than in normal or small strains of mice when comparisons are made at the same age during the period of rapid growth. Sutherland *et al.* (1974) suggested that the increased appetite of large mice is more than sufficient to compensate for the small increases in maintenance over small mice of the same age. More net feed is available for tissue growth and therefore better efficiencies are observed. Webster (1981) points out, however, that: "...the metabolism of an animal is not so much driven by the amount of energy flowing into the system but pulled along by the requirement of different organs and tissues for energy substrates...". The better gross efficiencies of larger strains simply reflects animals with the genetic potential for faster rates of tissue deposition. Roberts (1981) demonstrated clearly that at the same weight large lines of mice both consume more feed and convert it more efficiently than randomly selected control lines.

Eisen (1976) summarized the literature relating to selection for growth in rodents with particular emphasis on changes occurring in growth curve characteristics. In general, selection has had little effect on age at point of inflection or the shape of the growth curve. The author concludes: "mere selection for body weight does not generally yield basic changes in the shape of the growth curve, even though alterations in rate of gain are readily observed. Where experiments were specifically designed to alter these patterns realized responses were small."

Figure 1 (Roberts, 1981) illustrates the general shape of the growth curve of mice lines selected up and down for 6 week body weight compared to a randomly selected control line. Asymptotic weight is reached by six weeks (42 days) of age in all lines. Similarly, feed intake peaks at this age and gradually declines over the remainder of the animal's life. Maternal variance (both genetic and environmental) contributes approximately 60% to the total phenotypic variance at 14 days, but declines to 20-25% by 42 days of age (Eisen, 1976).

II. Genotype x Diet Interaction

A controversial area in animal breeding has been concerned with the type of environment most suitable for selection. The difficulty of interpretation and comparison of experiments with small numbers of animals

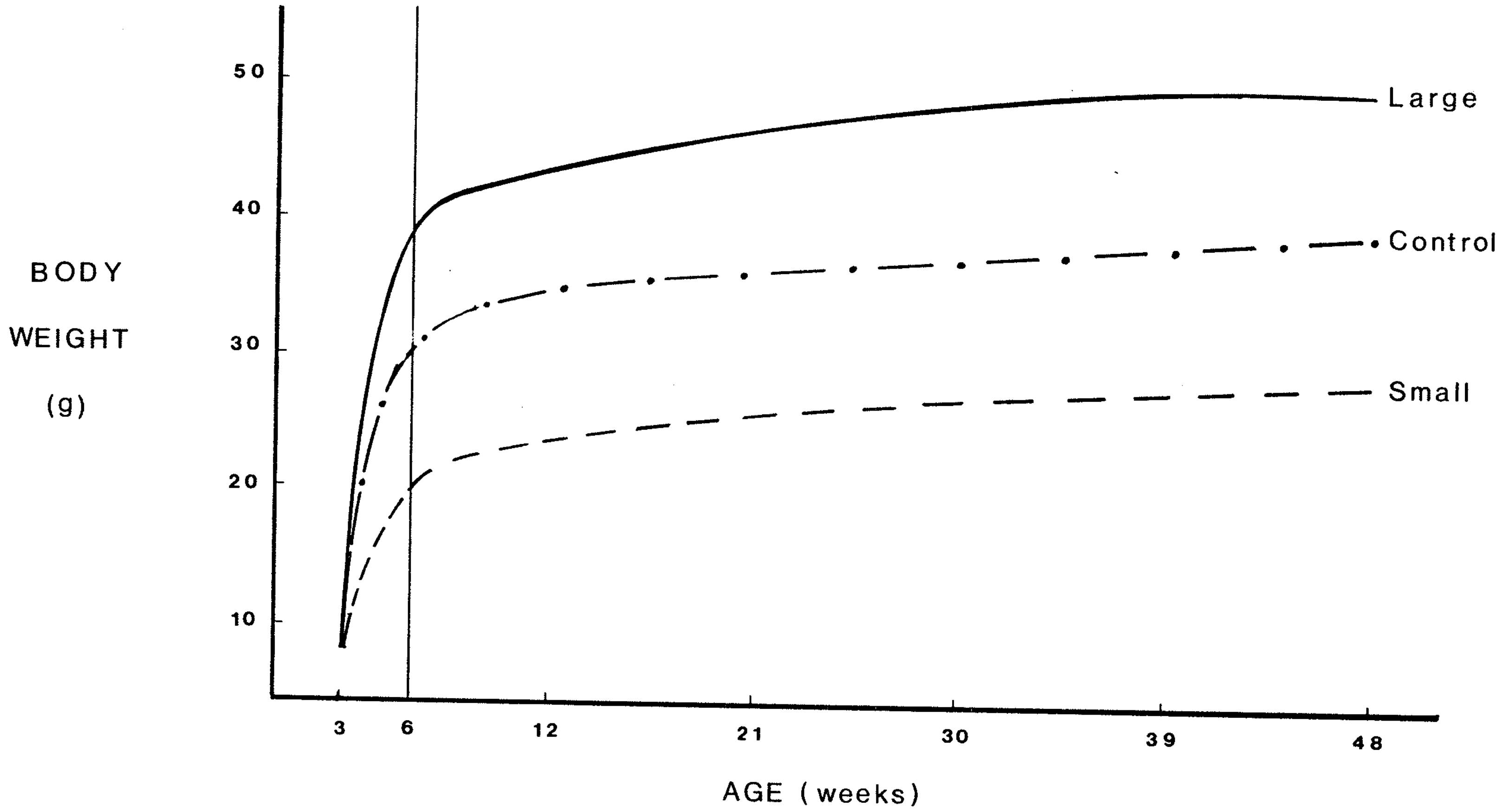


Figure 1. The growth curve for lines of mice selected up (large) and down (small) for six week body weight when compared to a randomly-mated (control) line (Roberts, 1981).

from different sources and with very different dietary conditions imposed during various stages of physiological maturity has contributed to the confusion in this area.

Three conflicting views have emerged. Hammond (1947) proposed that selection should be undertaken under circumstances "where the environmental conditions are optimal for the development of the character in question." He felt that desirable genes would be lost in an environment unsuitable for their expression. Roberts (1965) concluded, from a review of experiments existing at the time, that genotype by diet interactions are not very important unless a "severe modification of the environment is invented." Falconer (1977), on the other hand, suggested that animals should be selected in the "environment in which they are expected to perform." Further, if animals were to be raised in a range of different environments then selection should occur in the poorest of those conditions.

A) Mice and Rats

The opinions expressed by Falconer (1977) were based largely upon two of his earlier experiments. Falconer and Latyszewski (1952) selected within litter for high six week weight in mice on either a full or a restricted (25% of *ad libitum* intake) feeding regime. Six pairs of mice in each line were mated in each of nine generations, the top pair of offspring for gain between 3 and 6 weeks of age in each family being selected. The base population was derived from an F1 cross of four highly inbred lines. Mice on restricted feed were individually caged. Heritabilities were .20 and .30 for the full and restricted lines respectively. Diet restriction reduced the phenotypic variance and therefore overall response was still more rapid in the good than in the poor environment. In the 5th, 7th and 8th generations, mice from each line were raised on the alternate feeding regime. Although the mice selected on the restricted regime did well on the full feed regime; those selected on *ad libitum* feeding performed poorly on the restricted regime. In addition, the restricted line was leaner than the full fed line when both were fed *ad libitum*.

In Falconer's second experiment (Falconer, 1960) two major modifications were made. Restriction was based upon energy dilution (50% inclusion in the commercial diet of indigestible ground oat husks) which, when fed *ad libitum* to the base population from 3 to 6 weeks, resulted in a 20% reduction in weight from those fed the undiluted diet. Secondly, progeny from second litter matings were reared on the alternate diet each generation. Within family, divergent selection (one male and one female selected from each of 12 first parity litters) for gain from three to six weeks of age was continued for 13 generations. The conclusions drawn from this experiment were identical to those of the initial experiment. The most favorable overall response was obtained with animals selected on the low plane of nutrition and these mice, when fed the undiluted diet were leaner than those selected and fed on the same diet. A behavioural pattern, discussed in a later paper (Falconer, 1977), was evident. Mice selected on the low dietary plane wasted less food on either the high or low density diet than those from the line selected on the higher energy ration.

Seventeen generations of mass selection for postweaning gain (three to nine weeks of age) was practised on rats fed a commercial diet (22%

crude protein) either *ad libitum* or restricted to 75% of *ad libitum* intake (Park *et al.*, 1966). Realized heritability on full feed was low ($h^2 = .11$) but higher than with the limited fed line ($h^2 = .06$). To estimate diet by genotype interaction rats were sampled from each line in several generations and grown on the alternative feed system. Although few significant interactions were obtained there was a tendency for the rats selected in a particular environment to do better in that environment than those selected on the alternate regime. Conclusions reached were considered tentative considering the low heritabilities and lack of replication.

Evidence for Roberts' (1965) view that diet is relatively unimportant for selection purposes was provided by Dalton (1967). In a study which essentially repeated Falconer's second experiment (Falconer, 1960), the problem of feed sorting was avoided by pelleting the diet. Divergent selection, within litter, for gain from 3 to 6 weeks of age in mice fed a normal diet (16.8% crude protein, 5.2% crude fibre) or a 70% cellulose diluted diet (5.2% crude protein, 48.6% crude fibre) was practised for twelve generations. As in Falconer's two previous experiments litters were standardized to eight (four males, four females) at birth. Measurements were taken on twenty families in each line. Temperature was maintained at $65^{o}F$ ($18.3^{o}C$). Genotype x diet interactions were estimated in generations four to twelve by using progeny obtained from second parity matings. Mice, from each line, were divided equally and fed either the diluted or the control diet. Realized heritabilities were similar for all lines ($h^2 \simeq .22$) except those selected for positive gain on the diluted diet ($h^2 = .03$). In spite of this, response in the second parity where progeny were fed both diets indicated no significant genetic (group mean) differences between those selected on the high or low plane of nutrition. The author concluded that the diet had little effect on the overall outcome of selection. Significant parity effects were reported. There was a relatively poor response in the second parity litters from lines selected for gain on the full diet compared to the first parity litters which were used to estimate heritabilities.

Bailey *et al.* (1970) examined the effect of mass selection for post-weaning gain (four to ten weeks) of rats fed either a commercial diet (28.8% crude protein, 9.3% crude fibre) or a 45% cellulose dilution of this diet (16.3% crude protein, 50.5% crude fibre). Replicate selection lines and controls were maintained on each diet. Litters were standardized at birth to six and the progeny were group fed. After five generations realized heritabilities were higher on the regular diet (.32 and .38) than on the restricted diet (.17 and .28). Genotype by diet interactions were estimated in generation five by mating sires from each line randomly to control females from both diets and measuring the response of the progeny fed the dam's diet (Test 1). This was then repeated (Test 2), using the same sires and new dams chosen as described above. Presumably these rats would reflect one half the genetic gain of their sires. Progeny of sires from the full-fed lines outperformed those from the restricted lines by 3.5% for males and 7% for females in post-weaning gain. Interaction effects of sire line by diet were not significant. Male progeny of specific sires, however, responded significantly differently between Test 1 and Test 2. Although not explicitly stated by the author, these results would tend to support Hammond's (1947) conclusion that an optimal environment is most suitable for selection purposes.

Saxton and Eisen (1984) have estimated variance components for diet by genotype interaction in a random mating population of mice (approximately 1000 mice used) where four male progeny from each litter were assigned in pairs either to a control diet (Purina Mouse Chow) or a 22% fat diet. Measurements taken included three week weight, six week weight, feed consumption and the weight of several carcass fat depots. Heritabilities for six week weight were .37 on the control diet and .43 on the high fat diet. For all traits, ..."additive direct genetic rankings were not significantly different for the two diets...". This would tend to support Roberts' (1965) hypothesis.

B) Other Monogastric Species

Few reports exist on genotype x diet interactions in commercial, monogastric species. Fowler and Ensminger (1960) described an experiment with swine full-fed a production diet or fed the same diet restricted to 70% of *ad libitum* intake. Group feeding was practised; but excessive trough space provided. Selection for nine generations was based upon an index which included the number of pigs born alive in a litter, the number of pigs weaned in a litter and individual average daily gain (ADG) from weaning to 150 pounds. Slightly higher heritabilities were obtained on the high plane (.52) than on the low plane (.49) diet. These were estimated from the ratio of total response to total selection differential because of an outbreak of enteritus affecting both lines in generation six. When animals selected on one diet were tested on the other diet the best performance (ADG) was obtained with those selected on the low plane but fed the high plane diet. It should be noted that from generation six to nine the low plane line showed little improvement in ADG and the high plane line obtained absolute gains by generation nine that were apparent in generation five. Nevertheless, Falconer's hypothesis (Falconer and Latyszewski, 1952) received some further support.

Other studies in swine where the emphasis was on comparison of breed and diet differences have generally supported Roberts' hypothesis (Roberts, 1965) that genotype by diet interactions are not that important. For example, data collected from 95 progeny representing a diallel involving Poland China and Yorkshire breeds fed low or high energy diets indicated no significant sire or dam breed by diet interactions for either growth or carcass traits (Kuhlers *et al.*, 1977). Other authors (Hale and Coey, 1963; King, 1963; Kuhlers *et al.*, 1972) have come to similar conclusions.

In a series of publications (Marks and Lepore, 1968a; Marks and Lepore, 1968b; Marks, 1971; Marks, 1978) the results of a long term experiment to investigate the effects of selection for four week body weight under two nutritional regimes in a population of Japanese quail have been described. One line (P) was fed a diet considered adequate in crude protein (28%); the other line (T) was fed a diet that contained 20% crude protein with the addition of .2% thiouracil (a growth inhibitor). A preliminary experiment (Marks and Lepore, 1968a) determined that the latter diet caused a 15-20% reduction in growth.

Reasonable heritabilities (.35-.40) were obtained in both lines up to 20 generations of selection. In subsequent generations the heritability in the P line declined but significant genetic improvement was still apparent at generation 40. The T line did not respond to selection after the 22nd generation. The author postulated (Marks, 1978) that initially major gene effects were being exploited in both lines. However, only the diet deemed adequate permitted the expression of minor gene effects which would be important in later generations. No crossover study was undertaken.

III. Feed Efficiency

Although a direct consequence of selection for growth is improved gross efficiency; a more appropriate method for identifying optimal feed converters might be to select directly for feed efficiency. The increased cost and labour associated with measuring individual feed intake would have to be justified by an expected substantial genetic improvement in biological efficiency and, ultimately, demonstrate net economic benefit. Feed efficiency is not a directly measurable trait, but must be estimated from the ratio of gain to feed or its inverse (Malik, 1984).

A) Energetic Interrelationships

A brief review of the underlying energetic and physiological principles governing growth is necessary. Koch *et al.* (1963) have summarized (Fig. 2) the major environmental and genetic factors influencing the measurement of gross feed efficiency. Clearly, the trait is complex involving several interacting factors. Of particular importance is the relative changes in these factors during growth.

Fowler *et al.* (1976) and Webster (1981, 1979, 1977) describe some important energetic relationships relating growth to feed intake, heat production

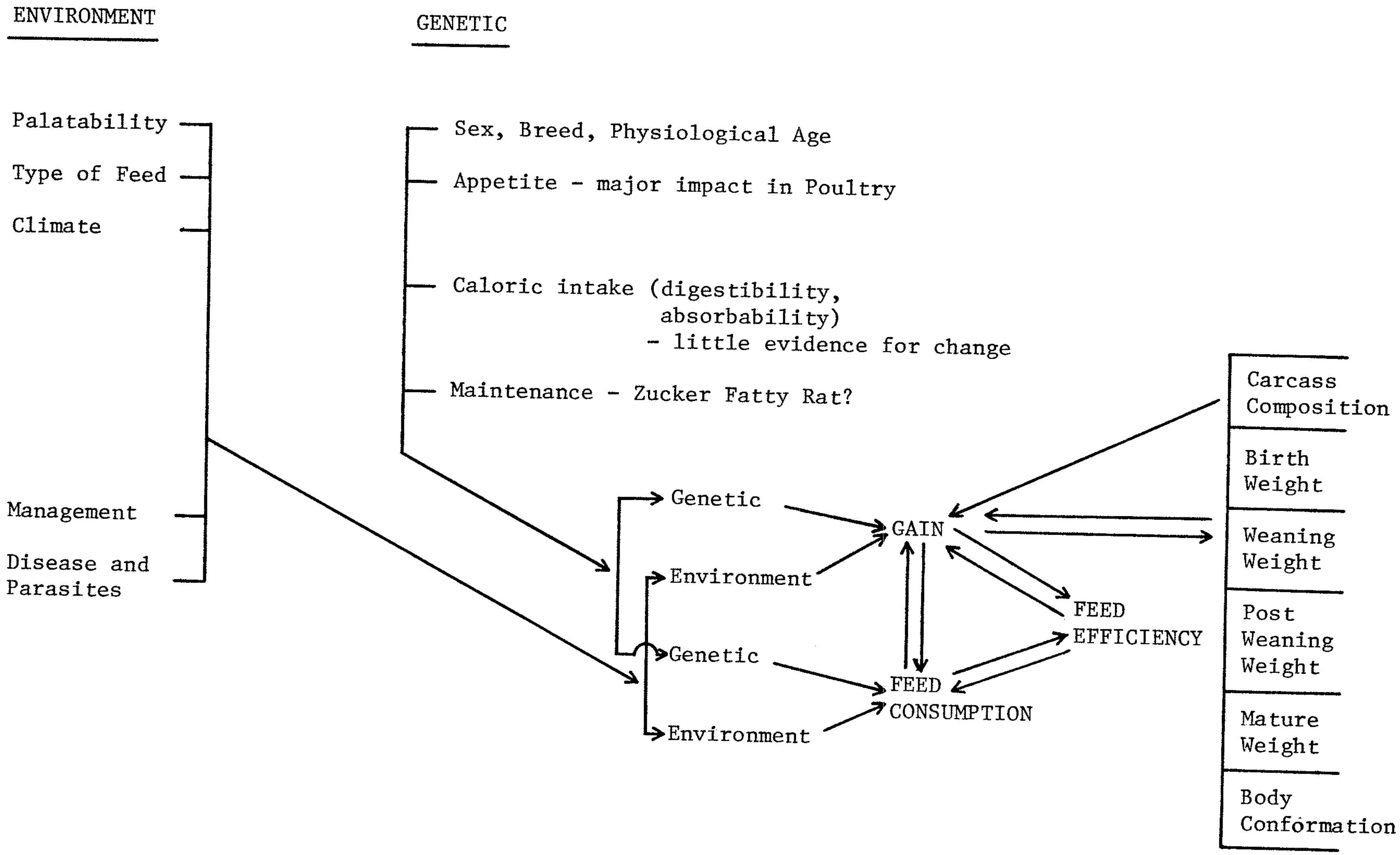


Figure 2. Environmental and genetic factors influencing gross feed efficiency (Koch et al., 1963).

and rates of tissue deposition (i.e. energy partitioning). These are illustrated in Fig. 3. During growth energy intake exceeds heat production until maturity is reached (Fig. 3a). The overall efficiency of energy retention reaches a peak at about 25% of mature weight and declines steeply thereafter (Fig. 3b). As an animal matures the weight gain per unit of retained energy declines (Fig. 3c) reflecting a shift from initial high rates of protein deposition to increasing rates of fat deposition. In simple terms, less mature animals gain rapidly; have low, but increasing relative maintenance requirements and therefore better apparent gross efficiencies (Fig. 3d) than larger animals. As animals approach mature weight it is conceivable that fatter individuals are more efficient (than leaner animals) since depositing fat, even though contributing inefficiently (relative to protein) to gain, would be favored over no tissue deposition at all (Roberts, 1981; Notter *et al.*, 1976). Stage of growth is, therefore, an important consideration in selection for feed efficiency. Appropriate adjustments to eliminate bias favoring environmentally less mature animals is essential.

B) Mice and Rats

Three strategies have been employed for studying the feasibility of selection for improved efficiency: selection for gross or lean tissue efficiency on *ad libitum* feed; selection for gain when a fixed amount of feed was offered either during a fixed time or to a fixed body weight; or employing an index method of selection.

Sutherland *et al.* (1970) demonstrated a significant response to selection for gross efficiency in mice when the trait was measured

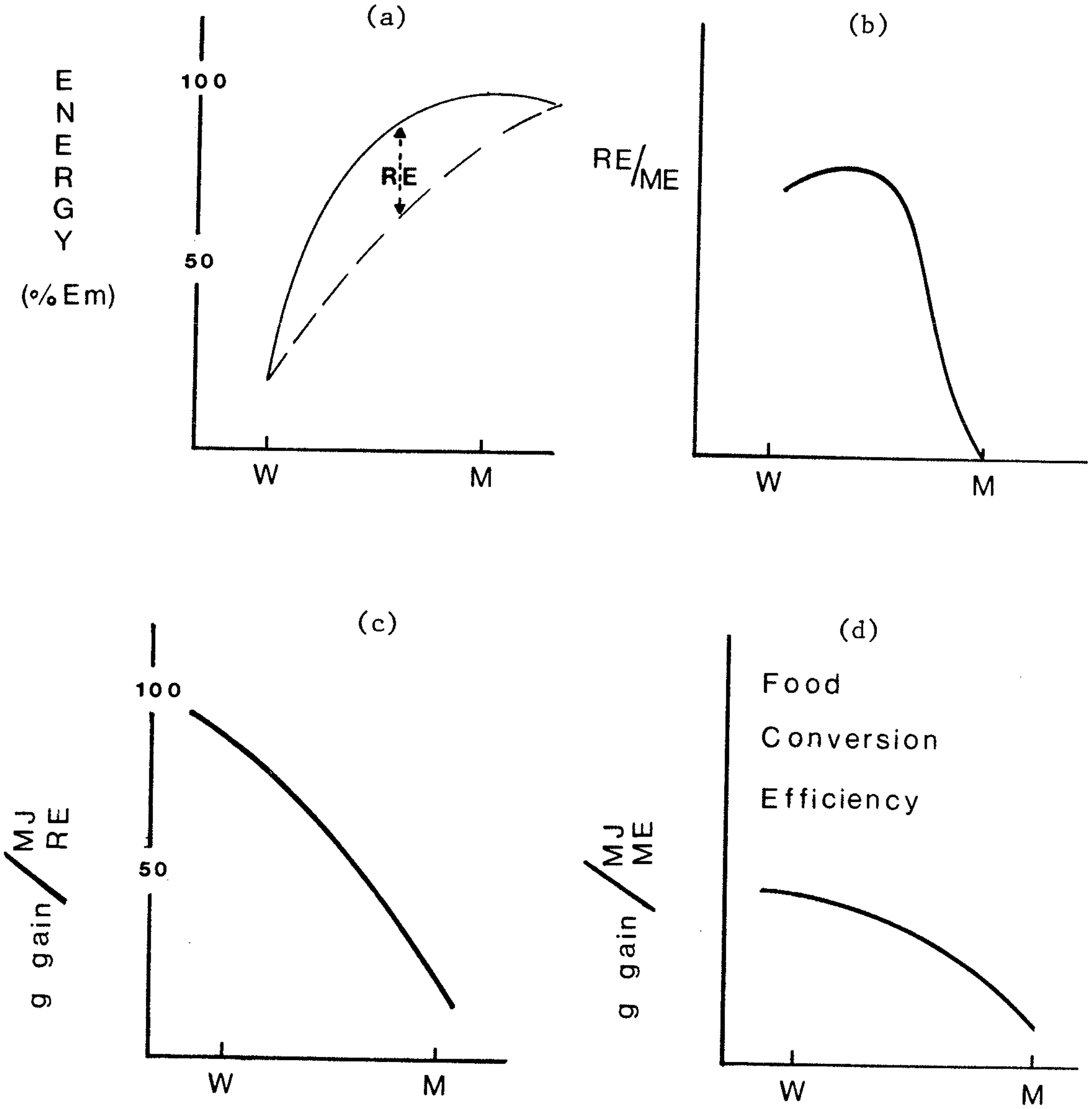


Figure 3. Factors affecting the efficiency of utilization of metabolizable energy (ME) for growth (Webster, 1979).

between four and eleven weeks of age. The heritability for efficiency was estimated to be .17 and the genetic correlation between gain and efficiency was .91. Small differences in response were noted between lines selected for gain, feed intake or efficiency.

More recent studies based selection on traits measured at a less mature stage of growth. Eisen (1977) used an index designed to maximize post-weaning gain (three to six weeks of age) while restricting the genetic response in feed intake to zero. A significant response in gain occurred with little change in feed intake up to the fourth generation. Feed intake then began to follow gain. The author speculated that a constant reevaluation of genetic parameters would be necessary to maintain the objectives of the index. Lin (1980), based upon a statistical argument, stated that selection on the feed to gain ratio itself would be more effective than the index method.

Notter *et al.* (1976) selected rats over five generations for rate and efficiency of protein gain from three to nine weeks of age. Selection was undertaken between full sib families where one female and two males were sacrificed for carcass evaluation. Realized heritability for lean tissue efficiency was estimated to be .18(±.16). Problems encountered with wide environmental fluctuations affecting between generation initial weights, final weights, feed intake and body composition were discussed in detail. The authors concluded, on a theoretical basis, that rather than select on an age basis, a constant weight interval would be more effective. They continue: "thus, selection for days to a constant weight, adjusted for effects of carcass composition on feed costs, could effectively improve growth efficiency during that weight interval without the use of feed records."

McPhee *et al.* (1980) designed an experiment with mice to select for post-weaning gain (five to nine weeks of age), linearly adjusted to initial weight on test, on a fixed amount of feed. Replicate selection lines and a randomly mated control line were maintained. The period of selection was considered a reasonable stage of growth for mice weaned at four weeks of age. An earlier experiment (McPhee and Neill, 1976) determined that protein deposited would increase 84% over this period. The fixed feed allotment was approximately 80% of that eaten by mice fed *ad libitum*. After six generations, realized heritabilities were .36 and .19 for the replicate lines. When fed *ad libitum*, these lines were 12% more efficient than the control lines but tended to be fatter at equivalent weights or ages. Although the diet contained 22% crude protein (gross energy, 17.4 MJ/kg) the authors recommended the use of higher levels of dietary protein in future experiments.

Yuksel *et al.* (1981) examined the effect of within family selection during two periods, three to five weeks (early) and five to seven weeks (late), for feed efficiency on fixed or *ad libitum* intake. The fixed intake was determined to result in a ten percent reduction in feed consumption from *ad libitum* fed animals. Selected lines were replicated. Heritability estimates, calculated as the ratio of total response to total cummulative selection differential, ranged from .08 in one late *ad libitum* line to .19 in one early *ad libitum* line. Absolute efficiency, at generation nine, was improved by 20% in the early lines over the control and by 60% in the late lines. The early lines tended to have lower initial weights. Response in the late lines to feed efficiency was negative at generation four, showing dramatic improvement in generations seven and eight. There was no interaction between feeding regime (early or late) and diet (*ad libitum* or restricted). Selected lines tended to be fatter than control lines.

Gunsett *et al.* (1981) selected mice over four generations for either maximum gain on a fixed amount of feed (100 g) or minimum feed intake for a predetermined gain (males: 20 g; females: 17 g). Initial weights on test were maintained at 10 g. Replicate lines, selected within full sib families, and a randomly mated control line were kept. Mice were weaned at 21 days. Realized heritability on fixed feed was .56 and on fixed gain, .73. In generation five growth curve parameters and net efficiency were estimated in all lines according to a method described by Park *et al.* (1966). Significant increases in mature weight and feed consumption over the control line were apparent. No differences in net efficiency of tissue deposition were detected. The authors stated: "these results suggest that the biochemical processes whereby energy is converted into growth have little additive genetic variation." Changes in gross efficiency were attributed to either reduced feed wastage or improved digestive efficiency. No information regarding carcass composition was reported.

Mass selection was practised for weight gain from 21 to 42 days of age in two lines, one full fed and the other restricted to 82% of *ad libitum* intake (Hetzel and Nicholas, 1982). Selected mice were chosen from twenty families (parents mated one male to two females). Two control lines were maintained (one on each diet) from ten single pair matings.

Realized heritabilities (response estimated as deviations from control) were .29 on full feed and .19 on restricted feed. Gain in the control lines declined over the seven generations of selection. Initial weights were lower and reproductive performance was poorer in the restricted lines compared to the control line. Absolute gain in the restricted line was similar in generation seven (≃ ten grams) to generation zero.

Parker and Bhatti (1982) did a more complex study with mice (placed on test at four weeks of age) fed either *ad libitum* or restricted (80% of full fed intake) and selected either after a fixed time (14 days) for feed efficiency or for gain after a fixed quantity of feed was consumed. A control line, fed *ad libitum*, was kept throughout the six generation duration of the experiment. Both restricted lines, fixed intake or fixed time, had higher realized heritabilities (.37 and .31 respectively) than either of the *ad libitum* lines (both .13). All selected lines tended to have smaller initial and final weights than the control line. No differences in carcass composition were observed. A crossover study indicated that mice selected on the restricted diet after a fixed quantity of feed was consumed were more sensitive to changes in dietary regime than the other selected lines.

C) Other Monogastric Species

Apparently the difficulties associated with measuring individual feed intake has limited the number of studies concerning selection for feed efficiency in either meat-type poultry or swine. Reviews by Yuksel (1979) on farm animals and by Pirchner (1982) on poultry emphasize the highly contentious nature of this obscure trait. Both express reservations about the ultimate value of selection for gross efficiency in view of the complications (i.e. environment by genotype interaction) inherent in its physical measurement and the uncertainty of the effects on correlated responses such as rate of gain or carcass composition.

The most favourable response to selection for feed efficiency has been reported for poultry. Wilson (1969) selected a broiler strain for gain from five to ten weeks or for feed efficiency over two generations. A randomly mated control line and replicate selection lines were maintained. A path coefficient method, used to describe partial correlations relating efficiency, feed intake, five week weight, ten week weight and average daily gain, enabled estimates of genetic parameters of feed efficiency independent of changes in the other traits. They concluded that selection for gain was only 75% as effective in improving efficiency as direct selection for efficiency itself ($h^2 = .39$).

Guill and Washburn (1974) selected for individual feed conversion during three generations either on a weight constant or a weight variable basis. Lines were derived from base populations that had either been randomly bred (RB) or selected for growth rate (GR) for ten generations. Differences between the weight variable and weight constant lines were small. Realized heritabilities were higher with lines derived from the RB population ($h^2 \simeq .50$) than from the GR population ($h^2 = .20$).

Pym and Solvyns (1979) described the results of selection for 5-9 week gain, feed consumption or decreased feed conversion ratio (grams feed/grams gain) over five generations with a broiler strain that had previously been selected (ten generations) for gain. A significant response in improved feed conversion ($h^2 = .21$) was correlated to the production of leaner carcasses when compared to the other selected lines. A similar biological response was extended to an economic evaluation (Flock and Marahrens, 1979) where improved net return was demonstrated with selection for feed conversion over selection for gain. This study was based upon two generations of selection.

The author is aware of few recent reports dealing directly and exclusively with selection for feed conversion in swine. Webb and King (1983) selected on the basis of pen group for feed conversion from weaning (50 days of age) to 82 kg. Boars were penned singly or in full sib pairs, and gilts in litter groups of up to four. Feed conversion was estimated for an individual as the group ratio of feed to gain when that individual within a pen reached the desired final weight. Selection operated for feed conversion on a between litter basis, with emphasis on gain being largely within litters. A randomly selected control was also maintained. After six generations of selection no significant realized response to feed conversion was obtained ($h^2 = .01$). Significant positive correlated responses, estimated as deviations from the control, were obtained with daily lean gain (≃ one standard deviation), daily feed intake (≃ .8 standard deviations) and adjusted backfat (≃ 1.2 standard deviations). Even with the admitted limitations of experimental design (no replication, selection criteria), the authors discourage the use of feed conversion as a trait in selection programs.

Several reviews (Fowler *et al.*, 1976; Tanksley, 1982; Jungst and Kuhlers, 1982) emphasize the theoretical consequences of recent physiological findings in relationship to efficiency. These have already been discussed. Population estimates of heritabilities for feed efficiency

(.31) in swine have been obtained and reviewed by Craft (1958). Robison and Burruecos (1973) estimated from 321 barrows representing 62 sires that average daily gain on test would be 112% as effective in improving feed to gain ratio as direct selection for the ratio itself.

IV. Mice as a Model for Growth in Commercial Livestock Species

Although extensive reviews (i.e. Eisen, 1976; Roberts, 1979) are available detailing the growth characteristics, including phenotypic and genotypic, direct and maternal interrelationships of mice few authors have attempted to contrast these to livestock species. For example, postnatal maternal influences on body weight are greater in mice than swine, rats or rabbits (Atchley and Rutledge, 1980). Steane and Roberts (1982) stated that although swine and mice are weaned at "biologically sensible" ages they (swine and mice) may not be "metabolically equivalent."

Roberts (1965) described the major contributions the mouse model has provided to further understanding of relevant factors in practical animal breeding. Those relating to meat production include:

1. The genetic variance in body weight and closely related traits is mainly additive.

2. Selection for this trait is effective and the response does not plateau, at least, until after 20 generations.

3. Caution is necessary in proposing selection programs particularly with regard to possible genotype by environment interactions and the effect of selection on correlated traits (i.e. carcass composition).

Eisen (1976), in addition to the above, noted the importance of the mouse for testing mathematical expectations with a biological model.

Perhaps the most significant, recent contributions are concerned with the effect of long term selection for body weight or gain on fundamental physiological and anatomical aspects of growth.

Selection for body weight, for example, has been shown to increase bone length and diameter (Hooper, 1977) and increase both muscle fibre size and number (Hooper and Hurley, 1983; Hooper and McCarthy, 1976). Correlated responses in organ (liver and kidney) and fat pad cell size and number, estimated in two independent lines selected for body weight, can be much more variable (Eisen and Leatherwood, 1978). Falconer *et al.* (1978), however, reported a linear increase in cell number and cell size of lung, liver, spleen and kidney in lines selected for high six week body weight.

An elaborate study (Falconer *et al.*, 1981) used combined embryos (mouse chimaeras) from pure and crossbred mice derived from lines selected either up or down for body weight or from an unselected control. Marker genes identified the source of individual cells in each chimaera and enabled estimates of the relative proportion of cells in several tissues which came from each parental type. Although body weight was linearly related to the mean proportion of "large" (derived from parents selected for increased body weight) cells in the whole animal; no single organ could be identified as a growth controller. Larger body weights were related to increased cell number; but this was not cell specific (i.e. the proportion of cells derived from larger strains did not increase). In addition, eleven day old embryos (before substantial organogenesis had occurred) of larger mice were heavier, independent of maternal effects, than smaller mice. The authors concluded that control of growth was systemic in nature.

Little evidence exists for significant phenotypic or genotypic variation in either apparent digestibility or net energy utilization in mice (Malik, 1984; Gunsett *et al.*, 1981; McCarthy, 1982; Stanier and Mount, 1972). This is consistent with reports in commercial livestock species (Nesheim, 1975) and in rats (Webster, 1977).

MATERIALS AND METHODS

I. Experimental Procedure

The principal question in this study related to the effect of diet on the outcome of selection for body weight or feed efficiency. Two hundred animals could be performance tested over a two week period simultaneously. These limitations on space, with the inclusion of two selection traits and three dietary regimes, required that the experiment be carried out in blocks or contemporary groups of three each generation. To facilitate ration preparation and feeding, each group represented one of the three dietary regimes. A control line fed a commercial diet common to all three groups was maintained.

A) Selection Experiment

1) Diets

Ward (1981) emphasized that little information is available on the nutrient requirements of mice during any stage of its life cycle. His survey of the literature, however, indicated that 12.5% available dietary crude protein (C.P.) was adequate for growth and 18% available C.P. permitted optimal breeding performance. These estimates were based upon a metabolizable energy of 2.9 Mcal/kg (~12 MJ/kg) in the diet. Reports by John and Bell (1976) and Bell and John (1981) indicated optimal levels of essential amino acids for growing mice. Diets were formulated in this study based upon these three reports.

To establish if any interactions exist between diet and genotype suitable ingredients had to be chosen. Corn and wheat are practical livestock grains commonly used in the industry. Rye was chosen because of its known antinutritional properties (Marquardt *et al.*, 1979). All three grains have different chemical compositions particularly with regard to type and amount of fibre. For a complete review of the relative effects of these grains on performance in livestock and laboratory animals see Antoniou (1980).

The diets, listed in Table 1, were formulated to contain 13% crude protein with a gross energy of 16.5 MJ/kg in the diet. Each ration consisted mainly of the particular grain, with minor adjustments (to equilibrate protein and energy) using soybean meal (48% C.P.) and tallow. A vitamin and mineral premix was also included (Table 2). These diets were fed only during the performance test. All mice when not being tested were fed a commercial diet, Purina Lab Chow (Table 3), that was purchased as required throughout the experiment.

All diets were fed in mash form after being finely ground in a Wiley Mill (screen size, 1 mm). Prior to the initiation of the study sufficient quantities of each grain and of soybean meal were stored ($10^{o}C$) to last the entire experiment. Complete diets were then mixed prior to each test period.

2) Breeding design

An overall outline of the breeding design is presented in Figure 4. The mice used in this study were derived from a large, outbred random mating population that had been maintained, without selection, for over

Table 1. Ingredient (g/kg) and nutrient composition of diets for each environment

Ingredient	Environment		
	Corn	Rye	Wheat
Corn (8.6%)*	830.0	-	-
Rye (13.0%)	-	930.0	-
Wheat (12.7%)	-	-	930.0
Soybean meal (48%)	120.0	20.0	20.0
Tallow	20.0	20.0	20.0
Dicalcium phosphate	5.0	5.0	5.0
Limestone	10.0	10.0	10.0
Vitamin mix	10.0	10.0	10.0
Mineral mix	5.0	5.0	5.0
Crude protein (g/kg as fed)	130.0	130.0	130.0
Gross energy (MJ/kg as fed)	16.6	16.6	16.5

*Crude protein of ingredients.

Table 2. Ingredient composition (per kg diet) of vitamin and mineral premix

Ingredient	Inclusion per kg of diet
Vitamin A	1,500 I.U.
Vitamin D	500 I.U.
Vitamin E	20 I.U.
Vitamin K	3.0 mg
Choline chloride	850.0 mg
Niacin	30.0 mg
Riboflavin	4.0 mg
Pyridoxine hydrochloride	1.0 mg
Folic acid	0.6 mg
Biotin	0.1 mg
Vitamin B_{12}	5.0 μg
Pantothenic acid	8.5 mg
Santoquin premix[1]	250.0 mg
Methionine[2]	3,000.0 mg
MnO	167.0 mg
ZnO	15.0 mg
$FeSO_4 \cdot 6H_2O$	31.0 mg
$CuSO_4 \cdot 5H_2O$	25.0 mg
NaCl (iodized)	4,762.5 mg

[1] Santoquin premix is an antioxidant.

[2] Methionine was added to supplement to requirement.

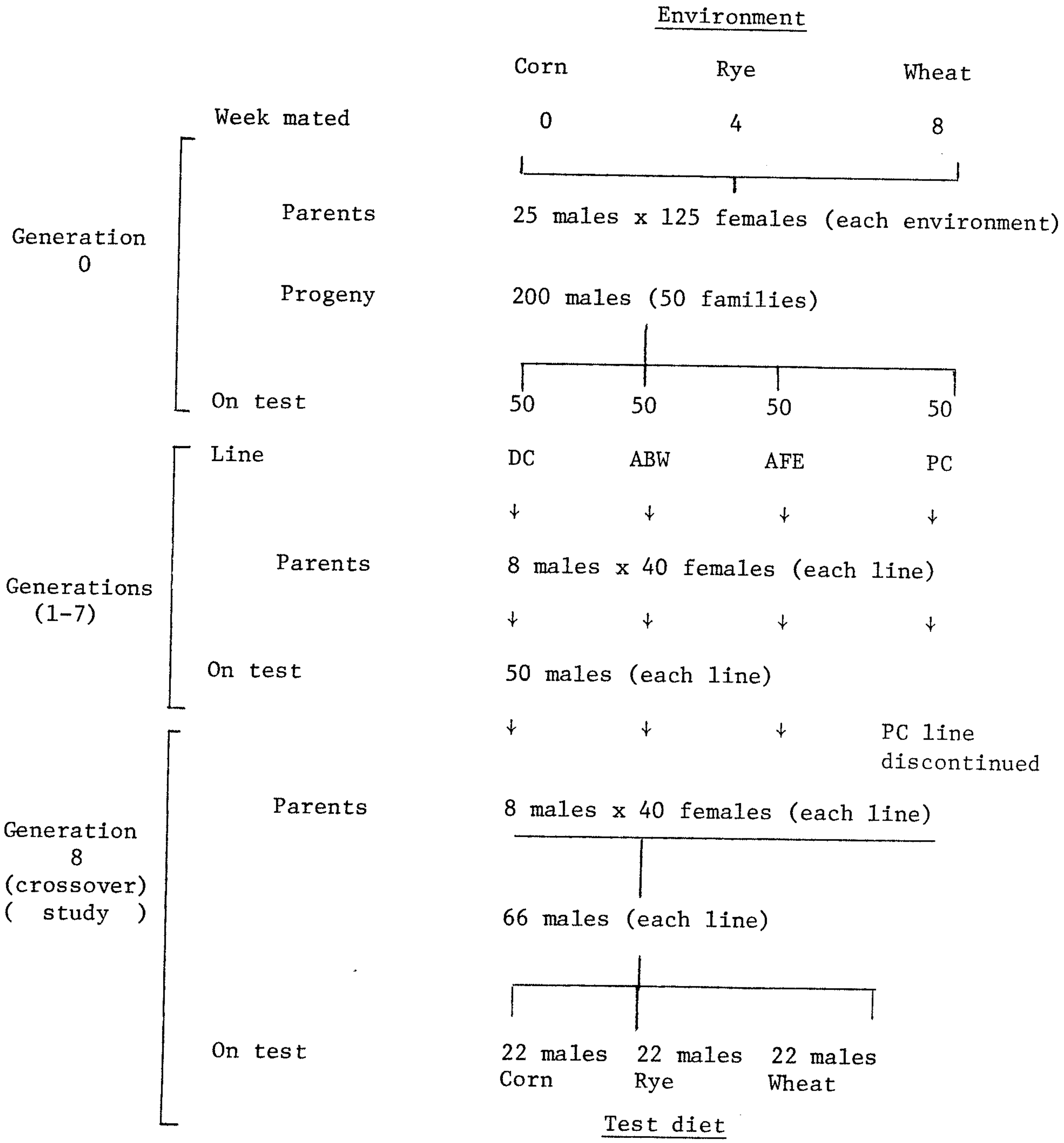
Table 3. Nutrient composition (g/kg) of commercial diets

	Purina Lab Chow[1]	F6 Rodent Blox[2]
Crude protein	246.0	240.0
Crude fat	54.0	60.0
Crude fibre	44.0	45.0

[1] Ralston Purina Company Inc. (450 Mountain Avenue, Winnipeg, Manitoba R2X 2Y8).

[2] Continental Grain Company (Chicago, Illinois 60606).

Figure 4. General outline of breeding design



50 generations. From the foundation population three breeding groups were established to represent the three dietary environments (E): corn (CE), rye (RE) and wheat (WE). The three groups, bred sequentially to enable staggered test periods, were each generated by mating 25 males with 125 females (one male x five females) randomly selected from the foundation population. Within each environment, 50 litters containing four or more male mice were chosen. One male from each litter was randomly assigned to one of four lines and placed on test. The three groups, each with four lines, became the base population (generation 0).

In subsequent generations (one to seven), eight sires from each line were mated to 40 dams (one male x five females). The five females in each cage were exposed to a male for a period of ten days and then placed individually into breeder cages. Males were introduced to females at eight weeks of age until generation three. Decreasing reproductive performance in all lines was observed and matings in subsequent generations were delayed until ten weeks of age. Full and half-sib matings were avoided.

Litters were standardized up to seven or down to eight when the progeny were three days old. All mice were weaned and toe-clipped for identification at 18 days of age. Conception rate (100 x # litters/40) and litter size were recorded.

3) Performance testing

A separate test room (apart from the breeding room) was established and equipped with supplemental heating to maintain the temperature between 26-27°C. With limited facilities and to maximize selection intensity, only male mice were performance tested. Females to be used for breeding purposes were randomly selected within each line each generation.

Plexiglass metabolism cages equipped with mesh (wire) lined tunnel feeders were specifically designed to measure individual feed intake, minimize feed spillage and allow for fecal collection. Any spillage that did occur was recovered by screen removal of contaminating fecal material.

At 21 days of age two male mice per litter from the first 25 litters in each line were placed in the individual feeder cages. Occasionally, 25 litters were not available and three mice would be selected from some litters. Initial body weight (g), final body weight (g) and feed intake (g) were recorded. In generation zero measurements were taken from 28 to 42 days. The rapid growth of mice in these conditions resulted in asymptotic weight being reached at 35 days of age. To maintain the selection objectives with their appropriate linear adjustments (refer to Selection Criteria), the test period was changed to 21-35 days of age in subsequent generations.

During generation seven, measurements were recorded weekly. Fecal material from each mouse on test was collected, dried and weighed to enable estimation of apparent dry matter digestibility. In addition, 20 mice were randomly selected from each line and maintained on the Purina diet until ten weeks of age when their individual weights (as an estimate of mature weight) were recorded.

4) Selection criteria

Within each environment (corn, rye or wheat) two selected lines were maintained. The traits of interest, final body weight (g) and feed efficiency (g gain/g feed intake), are at this stage of growth highly dependent on initial weight on test, a trait which is largely a reflection of maternal ability. To minimize maternal effects, while maintaining the performance test at a relevant (i.e. to livestock) stage of growth, adjustments for each trait were made by selecting those mice with the greatest positive deviation from the line representing the linear regression of final weight or feed efficiency on initial weight. The two lines generated were designated either the adjusted body weight (ABW) or the adjusted feed efficiency (AFE) line. The highest ranking eight male mice were selected as sires for the next generation. The proportion of the parent population selected was .53 (i = .75). In general, mass selection was practised. However, to minimize inbreeding, if more than one set of full brothers was among the top eight than one of the two subsequent brothers would be discarded in favor of a slightly lower ranked male.

Two control lines, randomly mated, were maintained in each environment. One line, the diet control (DC), was fed the same diet as the selected lines and identified as either the corn control (CC), the rye control (RC) or the wheat control (WC). To obtain data from large enough numbers of mice for half-sib estimates of genetic parameters, a second control line, fed the commercial diet was maintained. It was designated the Purina Control (PC) line and was included in each environment, each generation. A secondary rationale for this line was to monitor the effects of our own diets on reproductive performance and growth during the entire experiment.

B) Crossover Study

In generation eight the Purina Control (PC) line was discontinued. To estimate the performance of mice selected on one diet (i.e. the corn environment) when fed the other two diets, a crossover study was initiated. At least 66 mice from each line within each environment were fed one of the three test diets (22 mice per diet). All 200 cages were utilized. Body weight (g), feed intake (g) and fecal output (g) were recorded between 21, 28 and 35 days of age. A summary of this design is included in Figure 4.

Just prior to the beginning of the eighth generation the commercial diet (Purina Lab Chow) used throughout the experiment was no longer available. Gestating and lactating dams for the crossover study were fed F6 Rodent Blox, whose nutrient composition is described in Table 3. Weaned mice from dams fed this diet were much larger at 21 days of age than those from previous generations.

II. Statistical Analysis

A) Selection Experiment

1) General descriptive model

General analysis of variances procedures (Snedecor and Cochran, 1967) or a generalized least square analysis (Harvey, 1960), appropriate for unbalanced data, were used to test the effects of treatments imposed during the experiment on direct and correlated traits. The following linear model, with appropriate modifications where necessary, was employed:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \delta_k + (\alpha\beta)_{ik} + (\beta\delta)_{jk} + (\alpha\beta\delta)_{ijk} + E_{ijkl}$$

where:

Y_{ijkl} = the 1^{th} observation for the i^{th} environment and the j^{th} line in the k^{th} generation.

μ = overall mean

α_i = the effect of the i^{th} environment

β_j = the effect of the j^{th} line

δ_k = the effect of the k^{th} generation

( ) = the effect of all two-way and three-way interactions

E_{ijkl} = independent normal random variable with mean zero and variance σ^2.

Multiple comparisons, with balanced data, on significant ($P \leq .05$) main effect means were performed using the S.N.K. test (Snedecor and Cochran, 1967).

The full model was appropriate for litter size data. Tests of hypotheses for conception rate were made using the three-way interaction term as the estimate of the error term. Least square means in the diet control (DC) lines were estimated, of course, by excluding the line and line interaction terms from the model.

2) Estimation of adjusted traits

Simple linear regression methods (Snedecor and Cochran, 1967) were used within each line, each generation to obtain a best fit line describing the relationship between body weight or feed efficiency and initial weight on test. To determine if the slopes (b) generated were affected by treatments imposed, an analysis of variance was performed using the general model with the following modifications:

i) The Purina line (PC) was not included.

ii) All main effects and two-way interaction effects were tested using the three-way interaction term as an estimate of random variation.

Data were then adjusted using the following formula:

$$ABW,\ AFE = Y - b\ (X-10)$$

where:

ABW = adjusted body weight
AFE = adjusted feed efficiency
Y = an individuals final weight (g) or feed efficiency (g/g)
b = regression coefficient
X = an individuals initial weight (g)

All data were adjusted to a common initial weight of ten grams. Since only environment effects were significant a mean regression coefficient (b) for each environment (i.e. corn, rye or wheat) was used to adjust the data.

The Purina Control (PC) line was treated independently. Data were adjusted using separate regression coefficients (b) for each generation and environment.

3) Heritability estimates

Estimated from the sire component of variance

Although slight variations in number of mice existed between environments and lines and from generation to generation, the overall design was reasonably balanced with a hierarchical structure. A nested analysis of variance was used to partition the phenotypic variance (σ_p^2) into observational components attributable to differences among progeny due to environments, lines, generations, sires (σ_s^2) and dams, σ_d^2 (Falconer, 1981). Heritabilities were estimated in the usual way ($h^2 = 4\ \sigma_s^2/\sigma_p^2$) and standard errors of these estimates were calculated according to Becker (1967). This analysis provided a pooled estimate and included only three lines (ABW, AFE, DC) of each environment. A second analysis was performed separately for the Purina control (PC) line pooled across environments and generations (ENVIGEN).

Realized Heritability

Realized heritability estimates were obtained according to a method described by Falconer (1981). Selection differentials were calculated as the within generation, line and environment deviations of the weighted mean performance of selected sires from the overall mean of the contemporary line. The weight given to each sire was proportional to the number of his progeny included in the performance test in the next generation. Since only males were selected and would contribute one-half of their genes to the subsequent generation, true selection differentials (TSD) were assumed to be one-half of that calculated. Cumulative TSD was obtained by adding the TSD of successive generations.

Response was estimated by the mean performance of the progeny of selected sires as a deviation from their contemporary diet control (DC). Cumulative response was obtained by adding these each generation. The realized heritabilities were estimated by the regression of cumulative response on cumulative, weighted TSD. Standard errors for the regression coefficients (i.e. realized heritability) were calculated using the general formula applicable to simple, linear regression (Snedecor and Cochran, 1967).

B) Crossover Study

To provide a descriptive summary of data in generation eight, a generalized least squares (Harvey, 1960) procedure was used according to the following linear model:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + E_{ijk}$$

where:

Y_{ijk} = the k^{th} observation of the i^{th} environment fed the j^{th} diet
μ = overall mean
α_i = the effect of the i^{th} environment
β_j = the effect of the j^{th} diet
$(\alpha\beta)_{ij}$ = the interaction effect of the i^{th} environment and the j^{th} diet
E_{ijk} = an independent normal random variable with mean zero and variance σ^2.

The analysis was performed separately for each selected line, ABW or AFE. Effects associated with contemporary groups were adjusted for by expressing each observation as a deviation from the mean of its own diet control. The data were arranged in two-way tables (3x3) showing means for each environment by diet. To identify consistent trends these means were compared using a common multiple comparison method, SNK (Snedecor and Cochran, 1967). Very minor imbalances of observations per treatment sub-class were accounted for by using the harmonic mean of cell size.

A further analysis was undertaken to test directly for genotype (i.e. environment) by diet interactions. A mixed model procedure (Goodnight, 1978) enabled variance component estimation of sire and sire by diet random effects independent of other fixed effects. The linear model employed was:

$$Y_{ijklm} = \mu + \alpha_i + \beta_j + \delta_k + (\alpha\beta)_{ij} + (\alpha\delta)_{ik} + (\beta\delta)_{jk} + (\alpha\beta\delta)_{ijk} + A_l\,(\alpha\beta)_{ij} + A_l\,(\alpha\beta\delta)_{ijk} + E_{ijklm}$$

where:

Y_{ijklm} = the m^{th} observation of the mouse from the l^{th} sire in the i^{th} environment and the j^{th} line fed the k^{th} diet

α_i = a fixed effect common to mice from the i^{th} environment

β_j = a fixed effect common to mice from the j^{th} line

δ_k = a fixed effect common to mice fed the k^{th} diet

( ) = the fixed effects associated with all interactions of main, fixed effects

$A_l(\alpha\beta)_{ij}$ = a random variable associated with mice from the l^{th} sire within the i^{th} environment and the j^{th} line, with mean zero and variance σ_s^2.

$A_l(\alpha\beta\delta)_{ijk}$ = a random variable associated with mice from the l^{th} sire within the i^{th} environment and the j^{th} line fed the k^{th} diet, with mean zero and variance σ_{sb}^2.

E_{ijklm} = an independent normal random variable with mean zero and variance σ^2.

RESULTS

I. General Descriptive Analysis

A) Effect of Environment and Generation on the Purina Control (PC) and the Diet Control (DC) Lines

The Purina Control (PC) line, randomly mated, was included in each environment for each generation to compare the overall performance of the formulated diets (corn, wheat and rye) with a commonly available commercial diet. Generation means of initial weight, final weight and feed intake for the Purina Control line are presented in Figure 5. No consistent effects of environment were apparent. Considerable variation in performance was evident across generations. From generation zero to three a notable decline in the absolute value of the three traits was observed. Performance improved in generations four and five and then declined somewhat in generations six and seven.

Similar patterns occurred in the Diet Control (DC) lines (Figure 6). Relative performance of these lines compared to the PC line did not change substantially over the seven generations. A new breeder diet introduced just prior to generation eight (crossover study) was probably responsible for the larger initial weights, final weights and feed intakes observed during the crossover study.

The general effect of the selection diets was reasonably consistent across generations and these are summarized in Table 4. Mice fed the corn diets grew faster with less feed and higher gross feed efficiencies then mice from the other two environments. Progeny fed the rye diet tended to grow slower during the test period and had the poorest

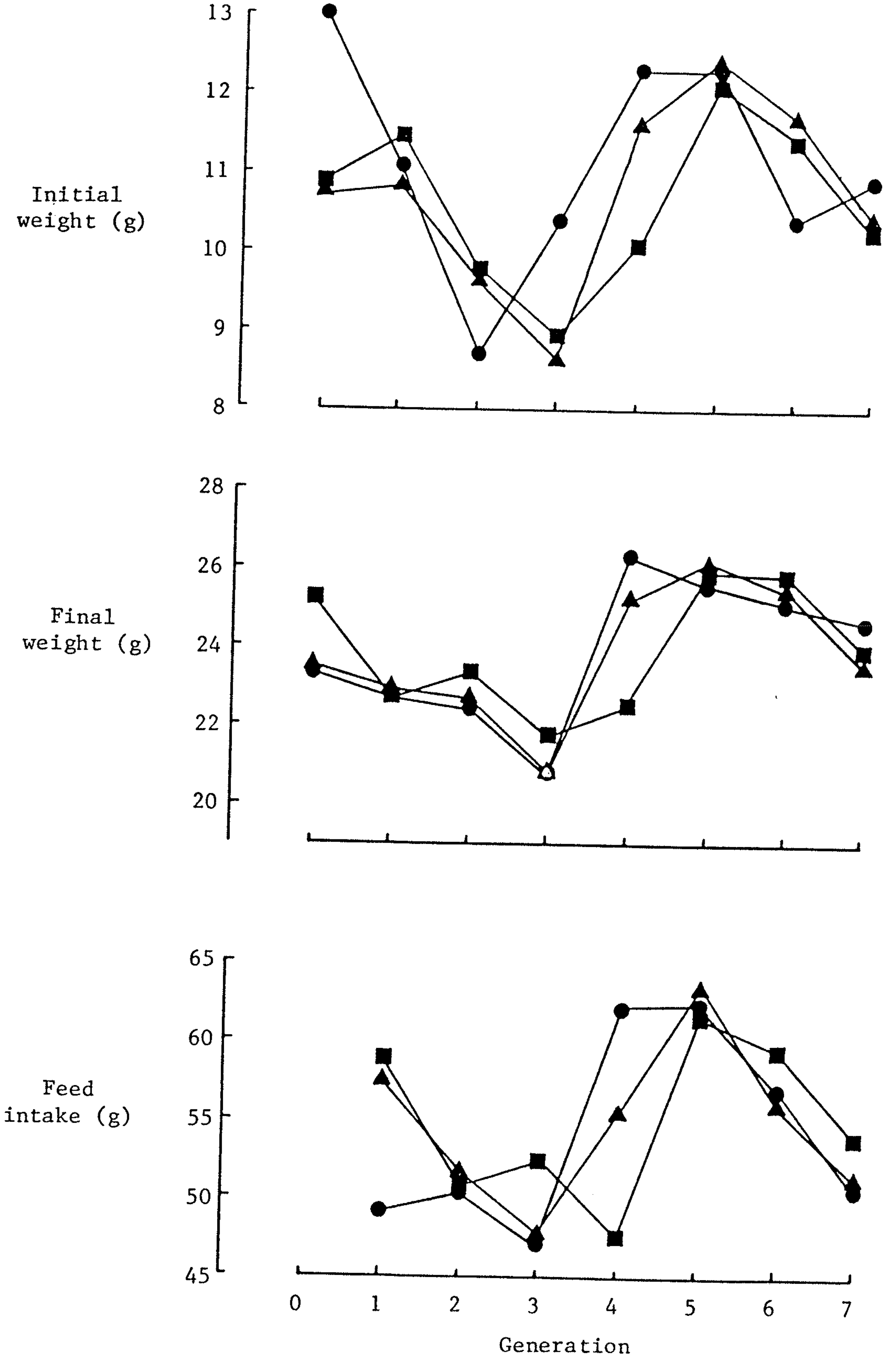


Figure 5. Generation means of initial weight (g), final weight (g) and feed intake (g) for the Purina Control (PC) line in the Corn ■ , Rye ● , and Wheat ▲ Environment.

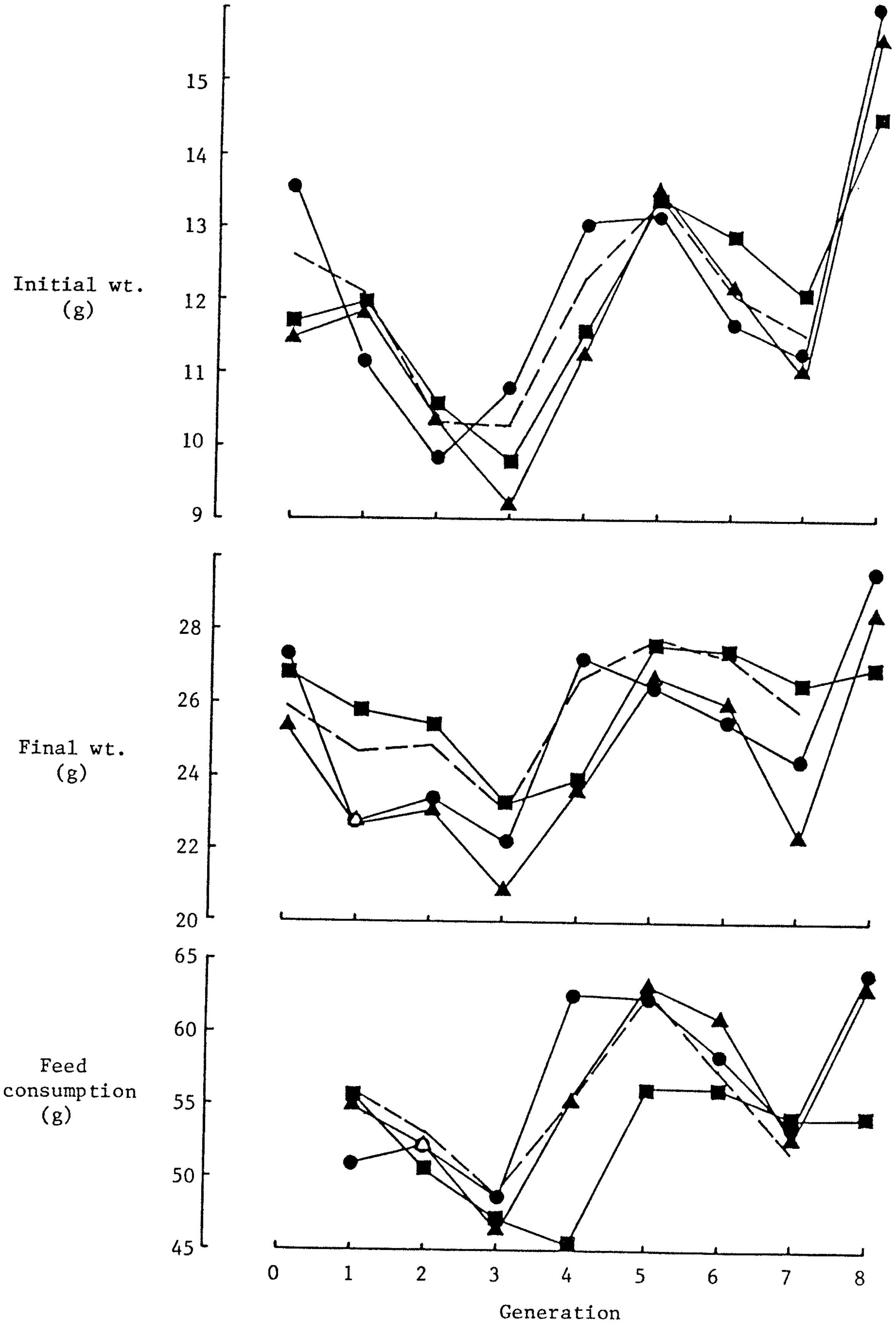


Figure 6. Generation means of initial weight (g), final weight (g) and feed intake (g) for the Diet Control (DC) lines in the Corn ■ , Rye ● and Wheat ▲ environments and Purina Control lines ---.

Table 4. Least square means of traits in the Diet Control lines in each environment estimated from generations one to seven

Envi.	Initial weight (g)	Final weight (g)	Feed intake (g)	Feed efficiency (g/g)
Corn	10.80	23.75	52.05	0.249
Rye	10.35	21.62	54.91	0.205
Wheat	10.58	22.80	55.52	0.221
S.E.	0.09	0.15	0.34	0.002

efficiencies. Those fed the wheat diet consumed as much feed as the rye-fed mice but converted it more efficiently and therefore had higher final weights.

B) Response to Selection

The initial test period of 21 to 42 days of age in generation zero was reduced to 21 to 35 days of age in subsequent generations. This was done to legitimize the selection procedure where linear adjustments for initial weight on test would only be appropriate during a linear phase of growth. The consequences of this alteration were, in some cases, dramatic. Although the complete seven generations are reported, response to selection was considered appropriate from generations two to seven only.

In Figure 7 the response in the adjusted body weight (ABW) lines to initial weight, final weight and feed intake, expressed as mean deviations from the contemporary diet control (DC) lines, are presented for each environment. In all environments there was a dramatic increase in feed intake and a more gradual increase in final weight on test initially. The response reached a peak and declined in later generations.

With the Rye Environment the response was rapid until generation four. In the Corn and Wheat Environment a more gradual response in final weight was maintained until generation five and the decline in subsequent generations was less severe than in the Rye Environment. Response in initial weight, although tending to follow the response in final weight, was less pronounced. At the end of generation seven end-of-test weights were approximately two, one and three grams larger than the Diet Control

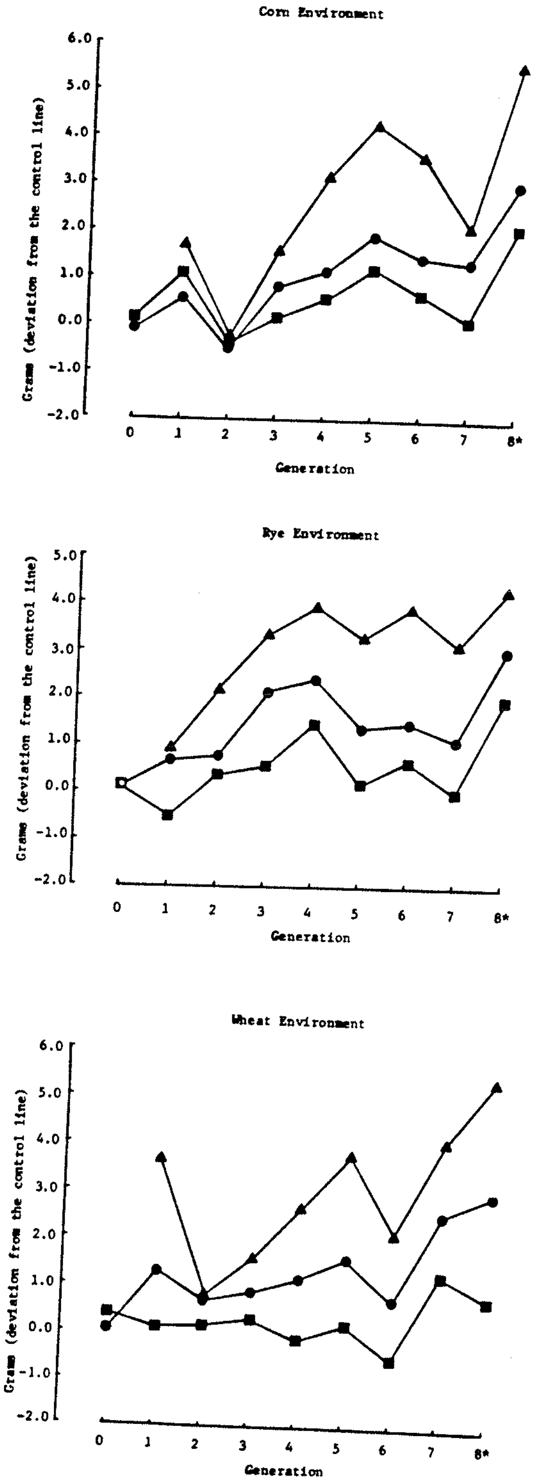


Fig. 7. Generation means (expressed as deviations from the Control line) of Initial weight (g) ■ , Final weight (g) ● and Feed intake (g) ▲ for the Adjusted body weight line.

*Generation 8 - crossover study (means of 3 diets).

lines in the Corn, Rye and Wheat Environments respectively.

Two major reservations concerning the comparison of absolute response across the three environments should be emphasized. As described above, the alteration of selection at 42 days in generation zero to 35 days in subsequent generations had a differential effect on lines in the three environments. Secondly, an inadvertent technical error resulted in a slightly negative selection differential for the ABW line in the Corn Environment during generation six (Appendix Table B9). This would essentially mean that this line was selected for one less generation when compared to the other two ABW lines.

Changes in the three traits with the adjusted feed efficiency (AFE) lines over the seven generations of selection were much more variable then with ABW lines, particularly in the Rye Environment (Figure 8). Little change occurred with initial or final weight on test from generations two to seven with mice fed the corn, rye or wheat diets. However, there was a tendency in the Corn Environment for a relative decline in feed intake in generation seven. This trend, more apparent in the Wheat Environment at an earlier stage (generation five), was most consistent in the Rye Environment beginning at generation three.

During the crossover study (generation eight), with the higher initial weights of all Diet Control mice (Figure 6), larger deviations from the contemporary DC lines were observed for all three traits with both selected lines (ABW and AFE) in the three environments (Figures 7 and 8). The deviations were more pronounced in the ABW line than in the AFE line.

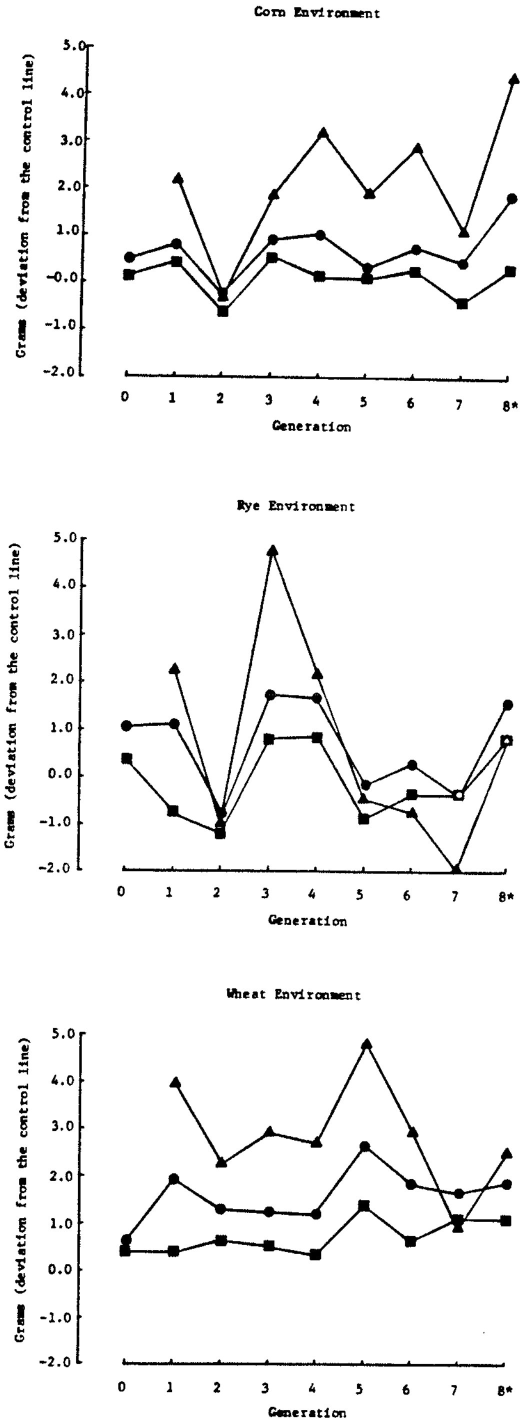


Fig. 8. Generation means (expressed as deviations from the Diet Control lines) of initial weight (g) ■ , final weight (g) ● and feed intake (g) ▲ for the Adjusted feed efficiency line in each environment.

*Generation 8 - crossover study (means of 3 diets).

C) Effect of Environment and Selection on Basic Reproductive Performance

Significant (P<.05) two-way interactions (Appendix Table B3) for litter size are graphically presented in Figures 9a, 9b and 9c. Although the variation between environments was higher in the DC and selected (ABW or AFE) lines than in the Purina Control (PC) line (Figure 9a), no consistent effects of diet (i.e. environment) are apparent. Overall mean litter size was 7.7.

Litter size each generation for either each environment (Figure 9b), or each line (Figure 9c) showed a similar pattern to the growth data in the control lines (Figure 6). Declining performance from generations one to three improved in generations four to six, with a slight decline in generation seven. Small litter size in the Wheat Environment in generations two and three (Figure 9b) was reversed in subsequent generations when lines fed this diet tended to have larger litters than mice fed the other two diets. In general, from generations four to seven, litter size with the selected and DC lines was higher than that obtained with mice fed the commercial diet (PC line).

Average conception rate over the entire experiment was 75%. A two-way interaction (Appendix Table B3) indicating a significant (P<.05) environment by diet effect is presented in Figure 10. Once again, similar to the growth data, but only with the Wheat and Rye Environments, lower conception rates were apparent from generations one to three, improved slightly and then declined in later generations. This trend was not evident with mice fed the corn diet. Conception rate increased from generations one

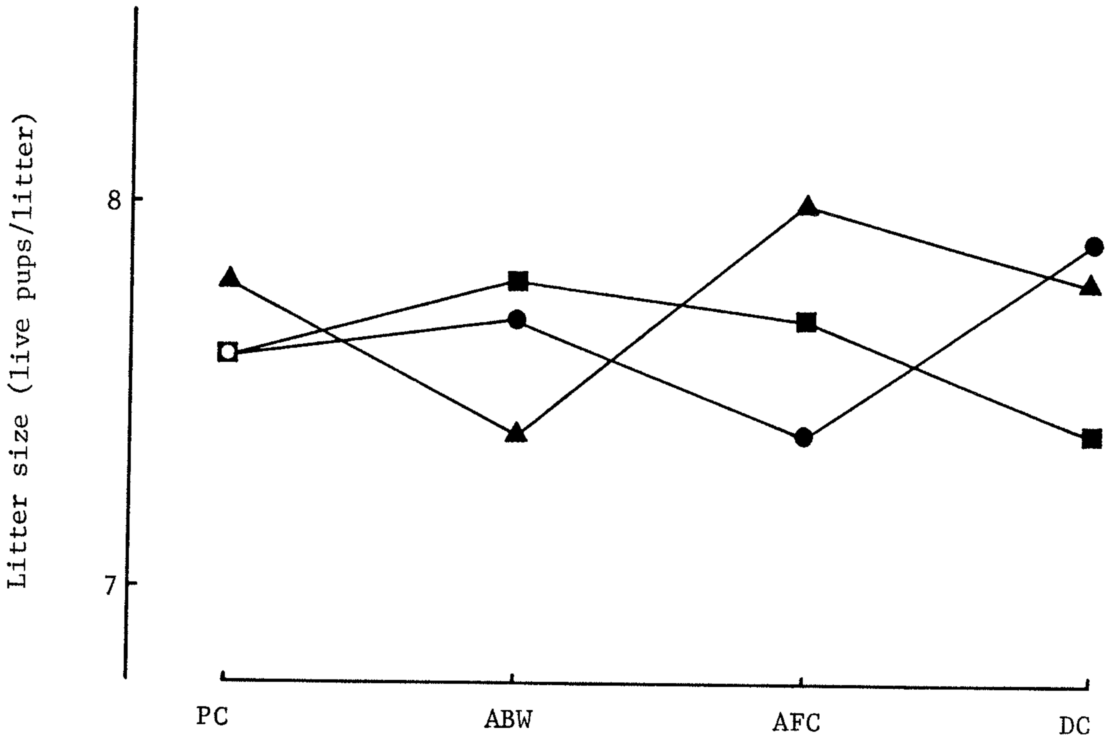


Figure 9a. Litter size for the Purina control (PC), Adjusted body weight (ABW), Adjusted feed efficiency (AFE) and Diet control (DC) lines in the Corn ■ , Rye ● and Wheat ▲ environments.

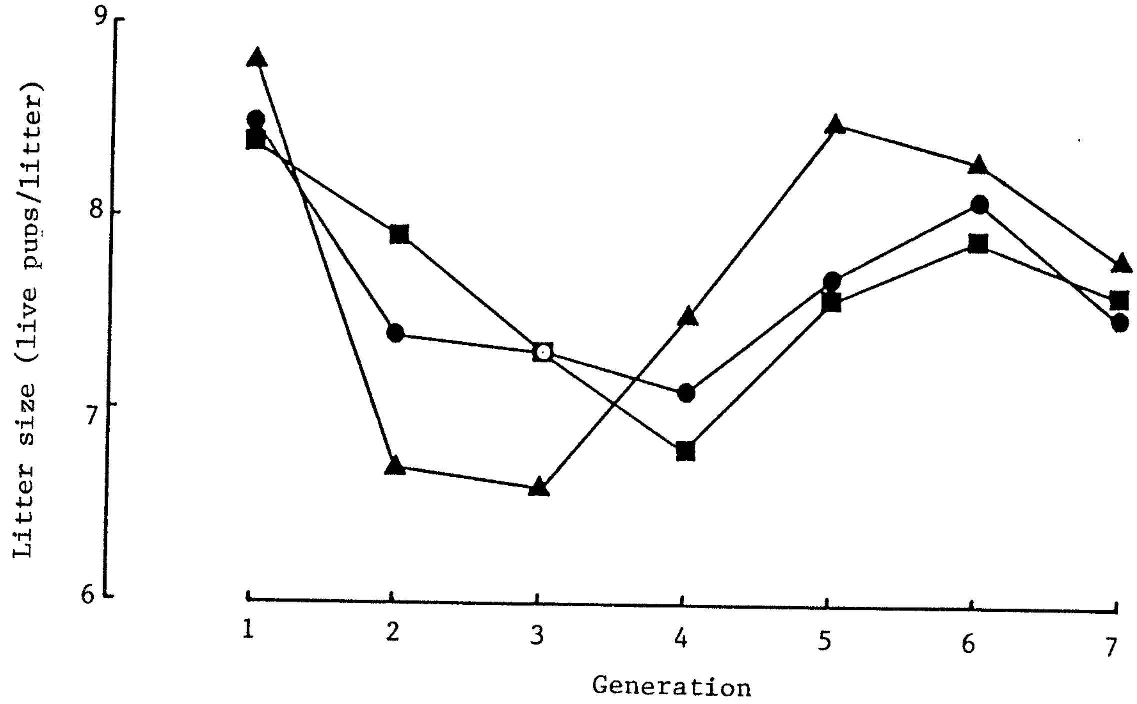


Figure 9b. Generation means of litter size in the Corn ■ , Rye ● and Wheat ▲ environments.

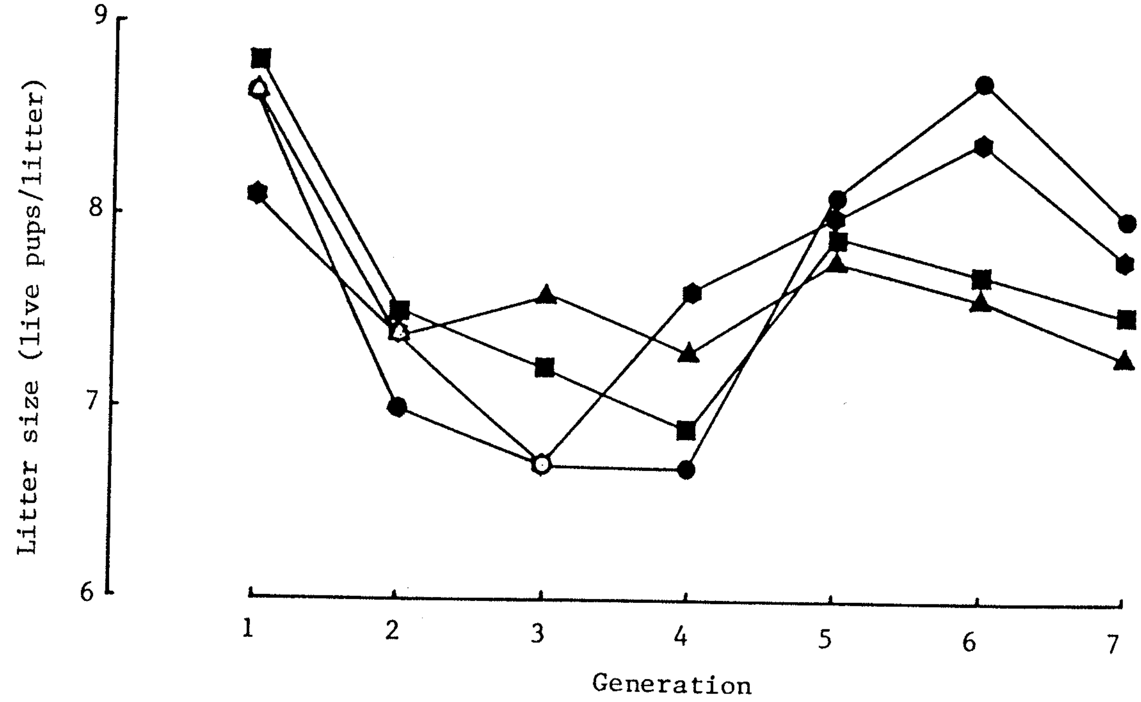


Figure 9c. Generation means of litter size for the Purina control ▲ , Diet control ● , Adjusted feed efficiency ⬢ and Adjusted body weight ■ lines.

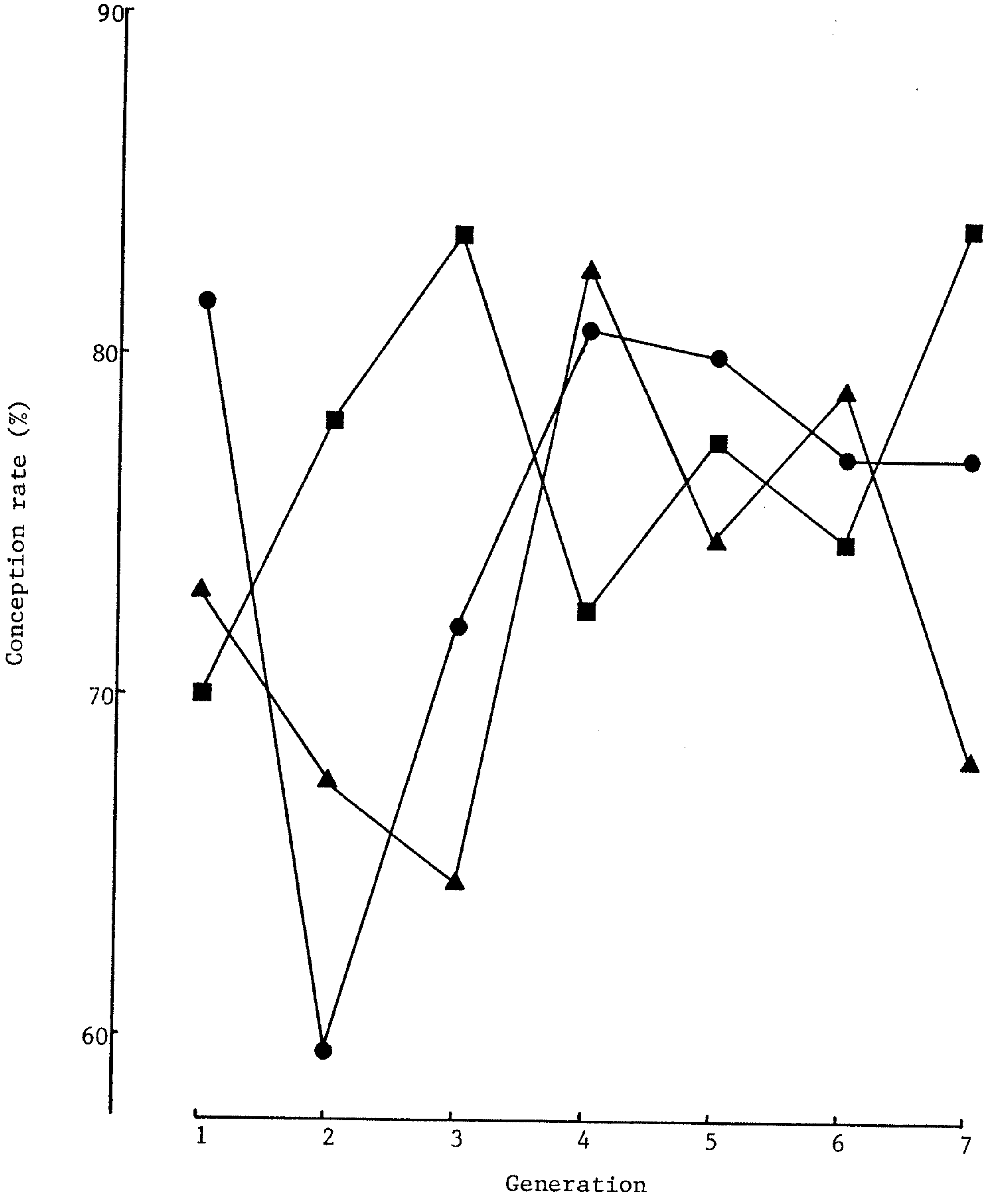


Figure 10. Generation means for conception rate (100 x # litter/40) for the Corn ■ , Rye ● and Wheat ▲ environments.

to three and, following a decline in generation four, continued to improve through to generation seven.

II. Quantitative Analysis

A) Parameter Estimates

In each of the diet control and selected lines linear adjustments of final weight, feed intake and feed efficiency were made for each generation to obtain within line comparisons of mice at a common initial weight. Slopes (b's) were generated and these were tested for the effect of environment, line, generation and all two-way interactions (Appendix Table B4). Only environment effects were significant ($P \leq .01$) for all three traits and these means are listed in Table 5.

Final weight and feed intake were more influenced by initial weight on test with mice fed rye and wheat than those fed corn. Feed efficiency was more dependent on initial weight with lines fed corn than in either of the other two environments.

Parameter estimates (Table 6) for the Purina Control (PC) line were analyzed separately (Appendix Table B5). Mean "b" values for final weight, feed intake and feed efficiency were .92, 1.76 and -.010 respectively. The estimates for feed intake and final weight were intermediate between those obtained with mice fed rye or wheat and those fed corn. Feed efficiency was equally dependent on initial weight with the commercial diet as with the corn diet.

Table 5. Means of regression coefficients (b) for estimating adjusted traits (ABW, AFI, AFE) in each environment

	Environment			
Traits	Corn	Rye	Wheat	S.E.
Final weight	0.80^A	1.13^B	1.12^B	.04
Feed intake	1.28^A	2.15^B	1.86^B	.13
Feed efficiency	-.010^A	-.006^B	-.005^B	.001

^{A,B}Means within rows followed by different letters are significantly different (P<.01).

Table 6. Parameter (b) estimates in the Purina Control line

	Trait		
Generation	Final weight	Feed intake	Feed efficiency
1	0.57^{A}	0.87	$-.012^{AB}$
2	1.08^{B}	2.03	$-.009^{AB}$
3	0.84^{AB}	1.75	$-.012^{A}$
4	1.14^{B}	2.25	$-.007^{B}$
5	0.84^{AB}	1.36	$-.008^{B}$
6	0.97^{AB}	2.18	$-.010^{AB}$
7	0.98^{AB}	1.88	$-.011^{AB}$
S.E.	.09	0.41	.001
Environment			
Corn	0.87	1.57	$-.010^{AB}$
Rye	0.99	1.77	$-.008^{B}$
Wheat	0.90	1.94	$-.011^{A}$
S.E.	0.06	.27	.001

[A,B] Means within columns followed by different letters are significantly different ($P \leq .05$).

B) Heritability Estimates

From the sire component of variance

In general, with the Purina Control line, the heritability estimates (Table 7) were low for all traits, particularly with final weight on test ($h^2 = .03$). Some improvement was observed with the adjusted trait, ABW ($h^2 = .13$). Feed efficiency had the highest heritability ($h^2 = .18$).

The Pooled Analysis (Table 7) for mice fed corn, rye and wheat diets resulted in a more predictable pattern, at least, with the unadjusted traits. A low heritability for initial weight ($h^2 = .06$) of mice at 21 days of age rose to a respectable .24 for final weight at 35 days of age. Adjustment of this latter trait (ABW) resulted in a decline in the heritability ($h^2 = .16$). The estimate for feed efficiency, $h^2 = .20$, was similar to the Purina Control line. When adjusted (AFE) a higher estimate ($h^2 = .28$) was obtained.

A more detailed description of the variance structure from the Pooled Analysis (Table 8) demonstrated a substantial reduction in the maternal contribution with both adjusted traits: 23.8% for final weight to 7.8% for ABW and 10.9% for feed efficiency to 0.0% for AFE. This did not result in a higher heritability for ABW because of a decline in the genetic variance for this trait when compared to final weight (23.8% to 15.7%). Phenotypic variance declined with the adjustment of the selection traits.

Realized heritability and correlated response

Realized heritabilities for the two traits (ABW and AFE) are shown in Table 9. The arithmetic mean realized heritability for the ABW line

Table 7. Half-sib estimates of heritabilities and standard errors ( ) in the Purina line or Pooled across environments and lines for selected and Diet Control lines

Trait	Purina	Pooled
Initial weight	.11(.17)	.06(.10)
Final weight	.03(.02)	.24(.08)
Feed efficiency	.18(.13)	.20(.08)
Adjusted body weight	.13(.11)	.16(.07)
Adjusted feed efficiency	.19(.10)	.28(.07)

Table 8. Phenotypic, genetic and maternal variances (σ_d^2) of all traits estimated from the Pooled analysis of variance including environments, lines (excluding the Purina line) and generations

	Variance		
	Phenotypic	Genetic (%)*	Maternal (%)
Initial weight (g^2)	2.8	0.2 (7.1)	2.1 (75.0)
Final weight (g^2)	8.0	1.9 (23.8)	1.9 (23.8)
Feed intake (g^2)	40.6	7.9 (19.5)	3.6 (8.9)
Feed efficiency $(g/g)^{2**}$	10.1	2.0 (19.8)	1.1 (10.9)
Adjusted body weight (g^2)	5.1	.8 (15.7)	0.4 (7.8)
Adjusted feed efficiency $(g/g)^{2**}$	8.5	2.4 (28.2)	0.0 (0.0)

*As a % of the phenotypic variance.

**Variance x 10^4.

Table 9. Realized heritabilities of selected lines in each of the three environments estimated from generations two to seven

	Environment		
Selected line	Corn	Rye	Wheat
Adjusted body weight	.24 (.06)[1]	.06 (.07)	.14 (.06)
Adjusted feed efficiency	.03 (.07)	.05 (.04)	.13 (.02)

[1] Standard errors in parenthesis.

across the three environments was .15. The highest heritability was obtained in the Corn Environment (h^2 = .24) with a realized response of .22 grams per generation (Table 10). The lowest heritabilities were found in the Rye Environment, with an intermediate response in the Wheat Environment. Correlated effects (Table 10) for adjusted feed intake (AFI) and adjusted feed efficiency (AFE) were all positive and followed closely the direct response to ABW in relative terms across environments.

The mean realized heritability for the AFE lines over environments was very low (h^2 = .07). The estimates ranged from a high of .13 in the Wheat Environment to a low of .03 in the Corn Environment (Table 9). Although correlated responses (ABW and AFE), Table 11, were positive in the Corn Environment, these tended to be zero or negative in the Rye and Wheat Environments. Of note is the dramatic decrease in AFI (feed intake adjusted to an initial weight of ten grams) in the Rye Environment, a similar but less pronounced trend occurring in the Wheat Environment.

Comparison of Realized and predicted response

Expected response per generation from the Pooled Analysis of variance can be estimated by:

$$\Delta G = i \times \sigma_p \times h^2$$

where ΔG = expected gain per generation

i = selection intensity = .75

σ_p = phenotypic standard deviation = 2.3 for the ABW lines and .025 for the AFE lines

h^2 = heritability = .16 for the ABW lines and .28 for the AFE lines

Table 10. Regression of response (as a deviation from the Control line) on generation number for lines selected for adjusted body weight in each environment

	Environment		
Trait	Corn	Rye	Wheat
ABW (g)	.22 (.06)[1]	.09 (.10)	.17 (.07)
AFI (g)*	.62 (.31)	.10 (.29)	.38 (.29)
AFE (g/g)	.003 (.001)	.001 (.001)	.002 (.001)

[1] Standard errors in parenthesis.

*Adjusted feed intake.

Table 11. Regression of response (as a deviation from the Control line) on generation number for lines selected for adjusted feed efficiency in each environment

	Environment		
Trait	Corn	Rye	Wheat
ABW (g)	.13 (.07)[1]	-.20 (.04)	.04 (.07)
AFI (g)*	.47 (.26)	-.80 (.20)	-.32 (.26)
AFE (g/g)	.001 (.001)	.001 (.001)	.002 (.001)

[1] Standard errors in parenthesis.

*Adjusted feed intake.

In the ABW lines, $\Delta G = .28$. This is reasonably close to that realized in the Corn Environment (.22 grams); but much higher than in the Wheat Environment (.17 grams) or the Rye Environment (.09 grams). Expected response per generation in the AFE lines was .005 grams per gram. This was not realized in any of the three environments.

C) Effect of Environment and Selection on Mature Weight

A surprising result was the effect of line on mature weight (ten week weight) estimated in generation seven (Table 12). Only line effects were significant ($P<.001$), environment differences being negligible (Table 12). The ABW and AFE lines were nine to thirteen percent larger than the DC lines. The differences between the ABW and the AFE lines, 4.4 grams and 3.2 grams heavier than the control respectively, were not significant.

D) Effect of Environment and Selection on Apparent Dry Matter Digestibility

Apparent dry matter digestibility was estimated in generation seven between 21 and 28 days of age (Dig. 1), 28 and 35 days of age (Dig. 2) and between 21 and 35 days of age (Dig. 3). Means of significant ($P\leq.05$) main effects are reported in Table 13. Some interactions were significant; however, these did not influence the relative rank between environments and lines.

The Rye Environment consistently had the lowest digestibilities. The Wheat Environment had lower values for Dig. 1 and Dig. 3 than the Corn Environment. Note the much lower digestibilities obtained at the

Table 12. Means of each line for mature weight (g) estimated as ten week weight in generation seven

	Line		
	ABW	AFE	Control
Mature weight	38.6[b]	37.4[b]	34.2[a]
S.E.	0.4	0.4	0.4

[a,b] Means followed by different letters are significantly different (P<.01).

Analysis of variance table

Source	df	Mean square	F
Environment	2	1.2	0.1
Line	2	291.2	26.8*
Environment x line	4	10.0	0.9
Error**	162	10.9	

*Line effect significant (P<.001).

**Missing data is responsible for the lower df for error.

Table 13. Effects of environment (A) and line (B) on apparent dry matter digestibility (%) between 21 and 28 days (Dig. 1), 28 and 35 days (Dig. 2), and 21 and 35 days (Dig. 3)

A. Environment

	Environment			
Trait	Corn	Rye	Wheat	S.E.
Dig. 1 (21-28 days)	80.0^c	75.8^a	78.3^b	.2
Dig. 2 (28-35 days)	72.4^b	70.5^a	72.2^b	.3
Dig. 3 (21-35 days)	76.3^c	72.9^a	75.5^b	.2

B. Line

	Line				
Trait	PC	ABW	AFE	DC	S.E.
Dig. 1 (21-28 days)	63.9^a	83.0^b	82.9^b	83.0^b	.3
Dig. 2 (28-35 days)	57.6^a	76.8^b	76.6^b	77.0^b	.4
Dig. 3 (21-35 days)	60.7^a	80.1^b	80.0^b	80.2^b	.2

[a,b,c] Means within rows with different letters are significant different ($P \leq .05$).

later stage of growth (Dig. 2) when compared to the less mature stage (Dig. 1).

No significant differences were apparent with the selected relative to the Diet Control lines. The Purina (PC) line had a 25% lower digestibility than the average of the other three diets.

III. Crossover Study

Table 14 lists the control line means of traits for each diet in each environment during generation eight. Initial weights on test, ranging from 13.1 grams to 15.4 grams, were much higher than in previous generations. This was attributed to a change in breeder and lactation diets necessitated by the sudden unavailability of the Purina diet used in previous generations. Final weights and feed intakes tended to be a little higher in the crossover study. Feed efficiencies, reflecting a later stage of maturity, were poorer than in previous generations (Appendix Tables C1, C2, C3). Digestibilities (% dry matter) averaged 80.0, 76.5 and 77.0 for the corn, rye and wheat diets respectively.

ABW Lines

Mean deviations (from their own diet control) of unadjusted traits in the ABW line are listed by environment and diet in Table 15. Mean deviations for initial weight across diets within environments should not have been significantly different. Unfortunately, due to sampling, the mice fed the corn diet in the Corn and Rye Environments tended to be larger than mice fed the other diets in each environment.

Table 14. Crossover Study. Control line means and standard errors of traits for each diet in each environment (Envi)

		Diet		
	Envi	Corn	Rye	Wheat
Initial weight (g)	Corn	13.1 (.3)	13.6 (.3)	13.9 (.3)
	Rye	14.5 (.4)	14.4 (.4)	14.9 (.5)
	Wheat	15.0 (.3)	15.4 (.3)	14.7 (.4)
Final weight (g)	Corn	24.6 (.6)	25.3 (.6)	25.0 (.4)
	Rye	27.3 (.4)	26.2 (.5)	26.0 (.4)
	Wheat	28.1 (.3)	27.5 (.5)	27.3 (.4)
Feed intake (g)	Corn	49.0 (1.5)	57.1 (1.5)	56.7 (1.2)
	Rye	60.0 (1.1)	65.2 (0.9)	63.8 (1.1)
	Wheat	62.2 (1.0)	69.2 (1.4)	60.1 (1.1)
Feed efficiency* (g/g)	Corn	23.5 (.7)	20.3 (.5)	19.8 (.6)
	Rye	21.4 (.7)	18.1 (.4)	17.3 (.7)
	Wheat	21.0 (.5)	17.6 (.5)	21.0 (.5)
Digestibility (%)	Corn	81.2 (.4)	77.5 (.5)	79.4 (.8)
	Rye	79.6 (.4)	76.1 (.4)	77.4 (.9)
	Wheat	80.1 (.2)	75.8 (.8)	75.0 (.4)

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*Feed efficiency (x 10^2).

Table 15. Crossover Study. Means (expressed as deviations from their own Diet Control) and standard errors for each diet in each environment (Envi) in the adjusted body weight line

A) Initial weight (g)
(S.E. = 0.3)

Significant (P<.0264) Envi x diet interaction.

	Diet		
Envi	Corn	Rye	Wheat
Corn	3.1*^{d}	1.8*^{bc}	1.5*^{abc}
Rye	2.6*^{cd}	2.0*^{bcd}	1.2*^{ab}
Wheat	1.0*^{ab}	0.2^{a}	1.1*^{ab}

*Mean deviations are greater than zero (P<.0001).

B) Final weight (g)
(S.E. = 0.5)

No significant effects.
Overall mean = 3.0.

	Diet		
Envi	Corn	Rye	Wheat
Corn	4.1*	2.7*	2.2*
Rye	3.0*	2.9*	2.2*
Wheat	3.5*	2.5*	3.0*

*Mean deviations are greater than zero (P<.001).

[a,b,c,d] Means followed by different non-capitalized letters are significantly different (P<.05).

Continued ....

Table 15 (Continued)

C) Feed intake (g) (S.E. = 1.3)

Significant ($P<.0243$) diet effect (S.E. = 0.8).

	Diet		
Envi	Corn	Rye	Wheat
Corn	8.8*	5.6*	2.3*
Rye	4.4*	3.7*	4.6*
Wheat	7.1*	3.2*	5.8*
Mean	6.8^{b}	4.2^{a}	4.3^{a}

*Mean deviations are greater than zero ($P<.001$).

D) Feed efficiency (g/g) (S.E. = .001)

Significant ($P<.0147$) Envi x diet interaction.

	Diet		
Envi	Corn	Rye	Wheat
Corn	$-.018*^{A}$	$-.004^{AB}$	$.004^{BCD}$
Rye	$-.010^{A}$	$.002^{BCD}$	$.014*^{CD}$
Wheat	$.015^{CD}$	$.022*^{D}$	$.009^{BCD}$

*Mean deviations are greater than zero ($P<.0061$).

[a,b] Means within rows followed by different non-capitalized letters are significantly different ($P<.05$).

[A,B,C,D] Means followed by different capitalized letters are significantly different ($P<.05$).

In spite of this no significant (P>.05) effects of environment or diet on final weight were detected. All mean deviations for final weight were significantly (P<.001) different from zero. A consistent trend, however, was that the largest mice within each diet were those mice selected on that diet. A general contrast procedure indicated that these mice were, in total, 2.9 (±2.2) grams heavier (P<.18) than the mice fed the two alternate diets.

Feed intake was significantly (P<.02) higher than the control for mice fed the corn diet than those fed either the rye or the wheat diet. All diets and environments in the selected line (ABW) consumed significantly (P<.001) more than their respective control lines. Feed efficiencies were more variable but tended to reflect each group's initial weight on test, the lower the initial weight the better the efficiency.

AFE Lines

Initial weights, expressed as deviations from the diet control, were more uniformly distributed within environments between diets (Table 16) in the AFE line than in the ABW line. The Wheat Environment had significantly larger (P<.05) initial weights than the Corn Environment. In general, there was a smaller response to initial weight in this line than in the ABW line.

There were no significant effects of either environment or diet on final weight on test. The pooled mean deviation was 1.7 grams; approximately one-half of that obtained with the ABW line. All means were significantly (P<.06) different from zero.

Table 16. Crossover Study. Means (expressed as deviations from their own Diet Control) and standard errors for each diet in each environment (Envi) in the adjusted feed efficiency line

A) Initial weight (g) (S.E. = 0.3)

Significant (P<.0306) Envi effect (S.E. = 0.2)

	Diet			
Envi	Corn	Rye	Wheat	Mean
Corn	0.6*	0.3	0.1	.3^{A}
Rye	0.8*	0.8*	0.6*	.8^{AB}
Wheat	1.1*	0.3	1.8*	1.1^{B}

*Mean deviations are greater than zero (P<.0969).

B) Final weight (g) (S.E. = 0.5)

No significant effects. Overall mean = 1.7.

	Diet		
Envi	Corn	Rye	Wheat
Corn	2.4*	1.0*	2.4*
Rye	1.2*	1.1*	2.1*
Wheat	2.1*	1.7*	1.6*

*Mean deviations are greater than zero (P<.0629).

^{A,B}Means within columns followed by different letters are significantly different (P<.05).

Continued .....

Table 16 (Continued)

C) Feed intake (g)
(S.E. = 1.2)

Significant ($P<.0021$) Envi effects (S.E. = 0.7).

	Diet			
Envi	Corn	Rye	Wheat	Mean
Corn	5.4*	3.5*	4.8*	4.5^{b}
Rye	0.5	-0.5	2.8*	$.9^{a}$
Wheat	1.6	1.9	4.4*	$2.6^{a,b}$

*Mean deviations are greater than zero ($P<.0224$).

D) Feed efficiency (g/g)
(S.E. = .006)

Significant ($P<.0001$) Envi x diet interaction

	Diet		
Envi	Corn	Rye	Wheat
Corn	$.008^{A}$	$.000^{A}$	.019*^{A}
Rye	$.004^{A}$	$.005^{A}$	.016*^{A}
Wheat	$.010^{A}$	.014*^{A}	-.018*^{B}

*Mean deviations are greater than zero ($P<.0213$).

^{a,b}Means within columns followed by different letters are significantly different ($P<.05$).

^{A,B}Means followed by different letters are significantly different ($P<.05$).

Feed intake (Table 16) was significantly ($P \leq .05$) higher in the Corn Environment than in the Rye Environment. The former group had the smallest initial weights (mean deviations) and therefore, in relative terms, gained more than the other two Environments. Feed efficiency (Table 16D) was significantly ($P \leq .05$) lower with mice fed the wheat diet in the Wheat Environment. This was also the group with the largest mean deviation for initial weight on test (Table 16A).

Sire Line by Diet Interaction

Variance components for sire line (ExL) and sire line by diet (ExLxd) for final weight, feed intake and feed efficiency are presented in Table 17. There was no evidence for genotype x diet interaction within sire lines; however the number of sires represented (49) was limited. Heritabilities, estimated from this analysis, were reasonable for final weight, somewhat low for feed intake and high for feed efficiency.

Table 17. Variance components and heritabilities estimated from a mixed model procedure to determine sire line by diet interaction

Variance component	Trait		
	Final weight	Feed intake	Feed efficiency[1]
Sire [environment (E) x line (L)]	.36	.42	.90
Sire [E x L x diet]	-.36	.14	-.01
Residual	5.45	34.82	5.73
h^2	.25	.05	.54

[1] Variance component x 10^4.

DISCUSSION

This study was unique in, at least, three specific aspects. Experiments on genotype by diet interaction have, historically, involved either dietary energy dilution or feeding on a restricted basis. With corn being the primary ingredient providing energy in practical poultry breeding rations, a concern was that long term selection might favour animals physiologically adapted to this specific grain type. The rations used in this experiment were formulated to provide approximately equal amounts of gross energy and crude protein. The only major distinction between the three diets was that the principle energy component was derived from either corn, rye or wheat. It should be emphasized, however, that the differences in nutrient composition of the three grains are predominantly related to the type and amount of dietary fibre (Antoniou, 1980).

Individual feeder cages were specifically designed to house mice in a small, production-oriented environment where feed intake could be measured accurately. The use of plexiglass materials enabled some visual contact between individuals in adjacent cages. Notter *et al.* (1976) used a similar design in their experiment with rats.

In this study, more emphasis was placed on attempting to mould the model (i.e. the mouse) to a stage of growth which would reflect energy utilization in practical livestock meat-type species. Although several authors have recognized the importance of temperature (i.e. Stanier and Mount, 1972) and stage of growth (i.e. Yuksel *et al.*, 1981); few have placed any importance on diet composition. Fewer still have considered these three environmental and physiological factors collectively.

I. Effect of Corn, Rye and Wheat Diets on Growth and Efficiency

The antinutritional properties of rye diets when fed to mice are minimal compared to other livestock species (Antoniou, 1980). For example, broiler chicken diets containing as low as 15% rye resulted in a significant appetite and growth depression (Marquardt *et al.*, 1979). Mice fed rye at 60% of the diet, on the other hand, showed no significant reduction in feed intake, weight gain or feed efficiency (McDonald *et al.*, 1974).

The diets based upon rye and wheat in this study consisted of 90% grain. The effect on growth traits of these two diets relative to the corn diet are presented in Table 18. Over the entire experiment mice fed the rye diet tended to have lower final weights, poorer gross efficiencies and reduced digestibility. Performance on the wheat diet was intermediate between rye and corn. The higher intakes on rye and wheat diets, indicating no effects on palatability, probably reflects the lower metabolizable energy values (i.e. higher fibre content) of these grains when compared to corn.

II. Response to Selection

The Adjusted Body Weight Line

The realized heritability for three to five week weight in the ABW line with mice fed the corn diet ($h^2 = .24$) was similar to the estimates obtained by Falconer (1960), $h^2 = .20$, and Dalton (1967), $h^2 = .22$, for

Table 18. Relative feeding value of rye and wheat expressed as a percentage of the response achieved with mice fed the corn diet

	Trait			
Diet	Final weight	Feed intake	Feed efficiency	Digestibility
Rye	-9.0	+5.5	-17.7	-3.4
Wheat	-4.0	+6.7	-11.2	-2.0

gain of full-fed mice between three and six weeks of age. Hetzel and Nicholas (1982) obtained a slightly higher heritability ($h^2 = .29$) with mice selected for gain during the same test period.

Realized responses in the Wheat Environment, with a heritability of .16, and, more particularly, in the Rye Environment ($h^2 = .06$) were poor. These estimates resembled more closely those obtained for mice and rats undergoing various forms of dietary restriction. Dalton (1967), Park *et al.* (1966), McPhee *et al.* (1980), Yuksel *et al.* (1981) and Hetzel and Nicholas (1982) describe lines selected for gain, while limiting energy intake; all having heritabilities less than .20.

Comparison of estimates of genetic parameters for different diets on traits measured between fixed ages may not be valid (Riska *et al.*, 1984). If, as Eisen (1976) has indicated, selection does not appreciably alter the shape of the growth curve, then relative mature weight between lines should be a good indicator of the effectiveness of selection. No differences between our lines selected for adjusted body weight in the three environments were detected. These lines were, however, much larger (~4 grams) than the randomly-bred control lines at ten weeks of age. Few other studies have reported mature weights. Parker and Bhatti (1982) found mature weights were directly comparable to final weight on test; but they used only one diet in their study.

A further confirmation of diet obscuring the true response was demonstrated during the crossover study when all mice had larger weaning weights. No differences in selection environment, as indicated by final weight on test, were distinguished. The diets were deliberately formulated to provide minimal requirements for postweaning growth. Perhaps all four diets (including the commercial diet) were inadequate for optimal growth of smaller mice at an early age. Progeny, however, weaned at larger body weights (during generation eight) would be more capable of expressing their improved genetic potential (relative to the control lines) for growth at this young age.

The Adjusted Feed Efficiency Lines

The response to selection for adjusted feed efficiency (AFE) was negligible in the three AFE lines representing the three environments. This was not typical of other experiments reporting selection for feed efficiency where heritability estimates ranged from .08 (Yuksel *et al.*, 1981) to .73 (Gunsett *et al.*, 1981).

Fundamental differences in design between this and other studies are readily apparent. For example, Sutherland *et al.* (1970) performance tested mice (already selected for gain for 20 generations) between four and eleven weeks of age and reported gross feed efficiencies as low as .047 for unselected, control mice. A significant linear decline in weaning weight (-.3 grams per generation) occurred over the 22 generations of selection for feed efficiency. Yuksel *et al.* (1981) described feed efficiencies of .004 in their late lines (selected from five to seven weeks of age) and .026 in the early lines (three to five weeks of age). The latter tended to have smaller initial weights after eight generations of selection. Both Parker and Bhatti (1982) and Hetzel and Nicholas (1982), after selection for feed efficiency between 21 and 42 days of age, report, as a correlated response, a decline in initial weight on test.

Two authors, recognizing the tendency for selection of this trait to result in smaller mice at weaning, used different strategies to avoid this correlated response. McPhee *et al.* (1980) employed a linear adjustment of feed efficiency to compensate for different start of test weights. With a test period of five to nine weeks of age, absolute efficiencies averaged .045 across his three lines. The most favourable outcome to selection for feed efficiency (either maximum gain on fixed feed intake or minimum feed for a fixed gain) in rodents was obtained by Gunsett *et al.* (1981). They insured uniformity of initial weight over generations by starting all mice on test at a common initial weight of ten grams. The interval of the performance test was equivalent to three to six weeks of age in the control line mice. Feed efficiency for this latter group was .061. Four generations of selection were used to make the estimates of genetic parameters.

All of the above studies report much poorer efficiencies, indicating a later stage of growth (Webster, 1981) than those consistently described in commercial, monogastric, meat-type species. Even in beef production (i.e. ruminant species) efficiencies under reasonable feedlot conditions range from .067 to .125.

The better efficiencies of selected mice at a relatively late stage of growth would identify animals that are either fatter (McPhee *et al.*, 1980; Yuksel *et al.*, 1981; Roberts, 1981; Notter *et al.*, 1976) or less mature (i.e. smaller weaning weights) in terms of relative growth rate (Webster, 1981; Fowler *et al.*, 1976).

A further complication with the mouse (as a model) might be the contribution of genetic variability in thermoregulatory processes that would affect energetic and gross efficiency (McCarthy, 1982). This would have important implications especially in studies where room temperatures were maintained at 20°C (room temperature). The thermoneutral zone of the single-caged mouse has been reported to be as high as 30-32°C (Mount, 1971).

During this experiment the temperature was maintained between 26°C and 27°C; a range at which thermoregulation would have a minimal influence on energetic efficiency. Gross efficiency was estimated at a less mature stage of growth and had values ranging from .179 to .281 (Appendix A4, A10), with an overall mean in the diet control lines of .249, .205 and .221 for the corn, rye and wheat diets respectively.

The data obtained for mature weight and in the crossover study might reflect a true correlated response to selection for AFE similar to that described with the ABW lines. The mean ten week weight of these mice was 3.2 grams heavier than the unselected, control mice and this did not depend on selection environment. During the crossover study the AFE lines, independent of selection diet, weighed, on average, 1.7 grams more than the control lines. This was consistent with a recent report in swine (Webb and King, 1983) where selection was carried out for improved feed conversion ratio on *ad libitum* feeding. They found no direct effect of selection for feed conversion, but a linear increase for the correlated response in gain.

Selection for feed efficiency has been successful in poultry (Guill and Washburn, 1974; Pym and Solvyns, 1979; Flock and Marahrens, 1979). All of these studies were based upon five or fewer generations of selection. Some experiments with mice have indicated that, where selection for feed efficiency was successful, the limits to response were achieved rapidly (Eisen, 1976) or showed improvement erratically and only in a few generations (Yuksel *et al.*, 1981).

III. Genotype by Diet Interaction

There were no significant genotype by diet interactions demonstrated in the crossover study. This is in general agreement with the theory expressed by Roberts (1965) that only with a severe modification of the diet would such interactions occur. However, with the ABW lines, there was a trend indicating that mice performed better with the diet they had been selected on. This is similar to the tentative conclusions reached by Park *et al.* (1966) with rats and by Fowler and Ensminger (1960) with swine. It could be argued that all three of the latter studies lend support to the hypothesis (Falconer, 1977) that recommends selecting animals in the environment in which they are expected to perform.

If genotype by diet interactions are important than one would expect that sires would rank differently depending on what they were fed. This was not apparent in our study or in the equivalent analysis described by Park *et al.* (1966). Bailey *et al.* (1970) did demonstrate a significant sire line by diet interaction. In unselected populations, response to selection would initially favour major genes affecting growth independent of diet; minor genes becoming more important in later generations (Marks, 1978; Roberts, 1981). If this is true then only subtle differences between diets would appear in the early stages of selection, with a more dramatic response after long term selection.

Falconer's two experiments (Falconer and Latyszewski, 1952; Falconer, 1960) contradict this hypothesis. However, as reported in a later paper (Falconer, 1977), there was a marked behavioural difference between lines of mice selected on diluted (Falconer, 1960) diets when compared to those selected on the regular regime. The mice selected on the low dietary plane wasted less food than their full-fed counterparts. A similar pattern, although not quantitated, was observed in the present study with all selected lines when compared to the randomly mated control lines. Dalton's experiment (Dalton, 1967) was designed to prevent this behavioural pattern by providing feed in a pelleted form. His crossover study indicated that diet had no effect on the overall outcome of selection.

Most of the studies reported in the literature have been plagued by problems. Dalton (1967), for example, tested diet by genotype interaction using second parity mice where the direct response to selection was poor compared to that demonstrated with first parity litters. Bailey *et al.* (1970) tested sire line by diet interactions after five generations of selection with progeny that would reflect only one-half the genetic gain (equivalent to two and one-half generations of selection) of their selected contemporaries. An enteritis outbreak (Fowler and Ensminger, 1960) in a selection experiment with pigs affected not only the response in the generation the disease occurred but in subsequent generations too.

Definitive conclusions are also difficult to arrive at in the present experiment. The nature of the design presented four major problems. Attempting to equate the biological model of the mouse to one that would be equivalent to a practical livestock situation resulted in low heritabilities similar to those described by Park *et al.* (1966) in their study with rats. Secondly, the size of the experiment, given the limitations of space and technical facilities, prevented the estimation of genotype by diet interaction over several generations. The complications associated with linear adjustments could have been avoided by using within litter selection. Finally, it would have been preferable to include the three diets in each contemporary group.

IV. General Discussion

Studies using feed efficiency as the primary selection objective have not been, with the exception of poultry, too promising. Some have been complicated by widely fluctuating start-of-test weights within and between generations (i.e. Notter *et al.*, 1976; Yuksel *et al.*, 1981; Parker and Bhatti, 1982). Both the comparisons between individuals and the estimation of realized response are confounded with the physiological bias inherent in our measurement of feed efficiency. Selection based upon unadjusted data with this trait favours animals with smaller start-of-test weights. Twenty-one or 28-day weights (weaning weights) are largely determined by environmental and genetic maternal ability (Eisen, 1976).

Studies with mice and rats were carried out during a stage of growth that is not representative of practical livestock species. Carcass composition differs during various stages of growth and, certainly, between species. The effect of selection of traits which are very sensitive to changes in energy partitioning might be unique for a particular species. An additional complication with mice is their relatively high lower critical temperature and the degree to which, at lower temperatures, physiological heat production (i.e. brown fat) and heat conservation (white adipose tissue) contribute to our overall measurement of gross efficiency. McPhee *et al.* (1980) and Yuksel *et al.* (1981) reported selected lines which were, indeed, fatter. Although the mouse has considerable importance as a pilot animal in many areas of research (page 22-24), studies concerned with feed efficiency may not be as valuable.

Feed efficiency is a complex trait (Koch *et al.*, 1963). Simple selection objectives emphasizing rate of gain (preferably age to desired weight) while limiting fat deposition are the most effective and direct methods for improving production efficiency (Roberts, 1979; Notter *et al.*, 1976).

Previous studies concerned with genotype by diet interaction involved some form of restricting energy intake. These practices would be cumbersome and labour intensive in practical breeding programs. Even if the advantages described by Falconer (Falconer, 1960) could be realized (i.e. leaner animals with greater adaptability) the system would be difficult to manage.

The feeding of various energy sources (i.e. grains) is a current common practice with the development of least cost ration formulation. The six selected lines, representing the three environments (grain types), were remarkably similar in mature weight at generation seven and in their overall response during the crossover study. Nevertheless, there was a tendency for improved performance of lines selected for adjusted body weight when fed their selection diet rather than the other two diets. After long term selection, when heritabilities decline and minor genes become more important (Marks, 1978) the differences could be more pronounced. The growth depressing effects of rye fed to commercial broiler chickens are more severe than observed with other species (Antoniou, 1980). This is a bird specifically adapted to consumption of highly digestible feedstuffs.

CONCLUSIONS

Specific

1. The realized heritability ($h^2 = .24$) for adjusted body weight obtained with mice fed the corn diet was higher than that estimated ($h^2 = .16$) using a half-sib analysis. Realized responses to selection with the other two diets were lower.

2. Selection for adjusted feed efficiency was not successful in improving this trait in any of the three environments.

3. Regardless of environment, the selected lines (both ABW and AFE) had greater mature weights than the unselected lines. During the crossover study, mice selected for ABW were, at 35 days of age, 3.0 grams larger than unselected mice; those selected for AFE were 1.7 grams larger than the diet controls. These data suggest that diet had little effect on the overall outcome of selection.

4. No consistent genotype by diet interactions were detected during the crossover study with either selected line (ABW or AFE). There was a trend in the ABW line for mice selected on a particular diet to perform better (final weight on test) when fed that diet compared to the other two diets.

General

Based upon the limited literature available and fundamental physiological arguments, selection for gross feed efficiency (or feed conversion) is, at best, labour intensive and, quite possibly, futile. Breeding programs emphasizing improvement in basic traits (e.g. fewer days to desired weight, reduced carcass fat) are more effective and predictable.

Genotype by diet interaction could be a fundamentally important concept in maintaining breeding stock that perform optimally in a specific environment or are adaptable to a wide range of dietary conditions. The problem would be better understood after long term selection (i.e. greater than 20 generations) and/or by using a base population that had already been selected for growth over several generations.

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Appendix A1. Generation(Gen.) means and standard errors for initial weight(g) in each of the three environments for the adjusted body weight(ABW) and the Control lines.

	Environment					
	Corn		Rye		Wheat	
Line Gen.	ABW	Control	ABW	Control	ABW	Control
0	10.94(.27)	10.69(.30)	10.61(.23)	10.45(.25)	12.85(.26)	12.59(.25)
1	12.13(.25)	11.02(.30)	10.39(.25)	10.88(.29)	10.37(.34)	10.20(.32)
2	9.20(.28)	9.63(.25)	9.79(.23)	9.41(.20)	8.94(.20)	8.75(.23)
3	8.87(.29)	8.81(.22)	8.80(.28)	8.22(.25)	10.11(.19)	9.82(.24)
4	11.22(.25)	10.64(.23)	11.74(.19)	10.30(.18)	11.98(.19)	12.10(.15)
5	13.72(.24)	12.44(.22)	12.58(.21)	12.45(.21)	12.47(.22)	12.26(.25)
6	12.50(.26)	11.87(.22)	11.75(.25)	11.23(.23)	10.19(.26)	10.71(.16)
7	11.27(.29)	11.17(.27)	9.96(.29)	10.03(.25)	11.51(.26)	10.23(.19)
8	15.64(.20)	13.52(.18)	16.57(.20)	14.62(.24)	15.80(.18)	15.04(.19)

Appendix A2. Generation(Gen.) means and standard errors for final weight(g) in each of the three environments for the adjusted body weight(ABW) and the Control lines.

	Environment					
	Corn		Rye		Wheat	
Line Gen.	ABW	Control	ABW	Control	ABW	Control
0	24.77(.43)	24.83(.40)	23.59(.31)	23.37(.35)	25.46(.35)	25.31(.31)
1	24.35(.37)	23.82(.38)	21.46(.46)	20.84(.51)	23.14(.41)	21.85(.42)
2	23.10(.37)	23.57(.40)	21.86(.41)	21.09(.37)	22.00(.38)	21.37(.37)
3	22.10(.39)	21.29(.40)	20.94(.47)	18.86(.42)	21.18(.38)	20.32(.42)
4	23.02(.35)	21.87(.37)	24.07(.38)	21.73(.38)	26.48(.35)	25.33(.33)
5	27.46(.33)	25.64(.33)	26.21(.39)	24.84(.29)	26.21(.31)	24.61(.34)
6	26.96(.33)	25.47(.31)	25.54(.50)	24.09(.44)	24.50(.47)	23.77(.24)
7	25.93(.34)	24.58(.47)	21.55(.42)	20.40(.44)	24.92(.36)	22.36(.32)
8	27.95(.28)	24.97(.30)	29.46(.33)	26.50(.26)	30.62(.30)	27.64(.24)

Appendix A3. Generation(Gen.) means and standard errors for feed intake(g) in each of the three environments for the adjusted body weight(ABW) and the Control lines.

	Environment					
	Corn		Rye		Wheat	
Line	ABW	Control	ABW	Control	ABW	Control
Gen.						
0	---	---	---	---	---	---
1	57.39(.84)	55.66(.88)	56.12(1.10)	55.26(1.08)	54.60(.79)	50.94(.99)
2	50.41(.72)	50.78(.73)	54.18(0.96)	52.08(0.92)	53.01(.87)	52.19(.79)
3	48.70(.79)	47.11(.78)	49.95(1.01)	46.61(1.11)	50.20(.81)	48.50(.87)
4	48.37(.68)	45.19(.76)	59.10(0.87)	55.17(1.00)	64.97(.77)	62.31(.83)
5	59.88(.92)	55.66(.72)	66.22(1.01)	62.96(0.88)	66.19(.66)	62.37(.83)
6	59.50(.72)	55.96(.69)	64.69(1.22)	60.72(1.09)	60.52(.98)	58.51(.56)
7	56.08(.70)	54.01(.93)	55.71(0.81)	52.67(0.98)	57.80(.88)	53.77(.71)
8	59.82(.80)	54.26(.91)	67.26(0.80)	63.02(0.74)	69.26(.80)	63.86(.83)

Appendix A4. Generation(Gen.) means and standard errors for feed efficiency(g/g) in each of the three environments for the adjusted body weight(ABW) and the Control lines.

	Environment					
	Corn		Rye		Wheat	
Line	ABW	Control	ABW	Control	ABW	Control
Gen.						
0	---	---	---	---	---	---
1	.213(.004)	.230(.005)	.197(.005)	.179(.006)	.234(.005)	.228(.005)
2	.275(.005)	.274(.005)	.223(.005)	.224(.005)	.246(.004)	.242(.004)
3	.272(.006)	.265(.004)	.243(.005)	.227(.005)	.220(.005)	.215(.004)
4	.243(.005)	.247(.005)	.208(.004)	.206(.003)	.223(.004)	.212(.002)
5	.230(.004)	.237(.004)	.206(.004)	.197(.003)	.208(.003)	.199(.003)
6	.244(.004)	.243(.004)	.213(.004)	.211(.003)	.236(.004)	.233(.002)
7	.263(.005)	.247(.006)	.208(.005)	.196(.004)	.232(.004)	.226(.003)
8	.206(.003)	.212(.004)	.191(.003)	.189(.004)	.214(.003)	.198(.003)

Appendix A5. Generation(Gen.) means and standard errors for adjusted body weight(g) in each of the three environments for the adjusted body weight(ABW) and Control lines.

	Environment					
	Corn		Rye		Wheat	
Line Gen.	ABW	Control	ABW	Control	ABW	Control
0	---	---	---	---	---	---
1	22.65(.29)	23.00(.31)	21.02(.36)	19.85(.38)	22.72(.33)	21.63(.34)
2	23.74(.33)	23.86(.33)	22.10(.33)	21.75(.32)	23.18(.30)	22.77(.25)
3	23.00(.31)	22.25(.29)	22.29(.34)	20.86(.36)	21.06(.31)	20.52(.28)
4	22.05(.33)	21.37(.32)	22.11(.31)	21.40(.32)	24.27(.28)	22.98(.27)
5	24.49(.29)	23.68(.26)	23.31(.33)	22.09(.26)	23.46(.26)	22.09(.21)
6	24.96(.25)	23.97(.27)	23.57(.34)	22.70(.30)	24.30(.33)	22.98(.19)
7	24.92(.28)	23.65(.40)	21.59(.29)	20.36(.32)	23.23(.28)	22.10(.20)

Appendix A6. Generation(Gen.) means and standard errors for adjusted feed efficiency (g/g) in each of the three environments for the adjusted body weight(ABW) lines.

	Environment					
	Corn		Rye		Wheat	
Line	ABW	Control	ABW	Control	ABW	Control
Gen.						
0	---	---	---	---	---	---
1	.235(.004)	.240(.004)	.199(.005)	.184(.005)	.236(.004)	.229(.004)
2	.267(.004)	.270(.005)	.222(.005)	.220(.004)	.240(.003)	.236(.004)
3	.261(.004)	.253(.004)	.236(.005)	.216(.005)	.220(.004)	.214(.004)
4	.255(.005)	.254(.004)	.218(.004)	.208(.003)	.234(.004)	.223(.002)
5	.267(.003)	.261(.003)	.221(.003)	.211(.003)	.221(.003)	.211(.002)
6	.269(.003)	.262(.003)	.223(.004)	.219(.003)	.237(.004)	.227(.002)
7	.275(.005)	.259(.005)	.208(.004)	.196(.004)	.240(.003)	.227(.003)

Appendix A7. Generation(Gen.) means and standard errors for initial weight (g) in each of the three environments for the adjusted feed efficiency(AFE) and Control lines.

	Environment					
	Corn		Rye		Wheat	
Line	AFE	Control	AFE	Control	AFE	Control
Gen.						
0	10.75(.27)	10.69(.30)	10.82(.23)	10.45(.26)	12.96(.25)	12.59(.25)
1	11.43(.21)	11.02(.30)	10.16(.20)	10.88(.29)	10.61(.26)	10.20(.32)
2	9.01(.27)	9.63(.25)	8.23(.28)	9.41(.20)	9.46(.26)	8.75(.23)
3	9.40(.23)	8.81(.22)	8.95(.22)	8.22(.25)	10.33(.23)	9.82(.24)
4	10.76(.28)	10.64(.23)	11.15(.14)	10.30(.18)	12.45(.17)	12.10(.15)
5	12.57(.18)	12.44(.22)	11.61(.18)	12.45(.21)	13.67(.21)	12.26(.25)
6	12.11(.23)	11.87(.22)	10.88(.19)	11.23(.23)	11.40(.23)	10.71(.16)
7	10.79(.22)	11.17(.27)	9.65(.20)	10.03(.25)	11.30(.22)	10.23(.19)
8	13.85(.20)	13.52(.18)	15.37(.18)	14.62(.24)	16.12(.22)	15.04(.19)

Appendix A8. Generation(Gen.) means and standard errors for final weight(g) in each of the three environments for the adjusted feed efficiency(AFE) and Control lines.

	Environment					
	Corn		Rye		Wheat	
Line Gen.	AFE	Control	AFE	Control	AFE	Control
0	25.38(.41)	24.83(.40)	24.44(.32)	23.38(.31)	25.85(.35)	25.31(.31)
1	24.65(.37)	23.82(.38)	21.92(.38)	20.84(.51)	23.67(.38)	21.85(.42)
2	23.21(.47)	23.57(.40)	20.30(.48)	21.09(.37)	22.64(.43)	21.37(.37)
3	22.22(.40)	21.29(.40)	20.57(.48)	18.86(.42)	21.61(.48)	20.32(.42)
4	22.94(.49)	21.87(.37)	23.39(.39)	21.73(.38)	26.52(.38)	25.33(.33)
5	25.97(.40)	25.64(.33)	24.71(.44)	24.84(.29)	27.23(.36)	24.61(.34)
6	26.26(.36)	25.47(.31)	24.34(.37)	24.09(.44)	25.62(.39)	23.77(.24)
7	25.05(.30)	24.58(.47)	20.07(.38)	20.40(.44)	23.99(.39)	22.36(.32)
8	26.86(.29)	24.97(.30)	28.01(.35)	26.50(.26)	29.45(.25)	27.64(.24)

Appendix A9. Generation(Gen.) means and standard errors for feed intake(g) in each of the three environments for the adjusted feed efficiency(AFE) and Control lines.

	Environment					
	Corn		Rye		Wheat	
Line Gen.	AFE	Control	AFE	Control	AFE	Control
0	---	---	---	---	---	---
1	57.82(0.80)	55.66(.88)	57.48(0.90)	55.26(1.08)	54.91(0.91)	50.94(.99)
2	50.42(0.85)	50.78(.73)	51.08(1.05)	52.08(0.92)	54.41(0.87)	52.19(.79)
3	48.95(0.82)	47.11(.78)	51.37(1.24)	46.61(1.11)	51.33(1.00)	48.50(.87)
4	48.40(1.07)	45.19(.76)	57.31(0.96)	55.17(1.00)	64.97(0.89)	62.31(.83)
5	57.58(0.85)	55.62(.72)	62.51(1.07)	62.96(0.88)	67.17(0.84)	62.37(.83)
6	58.85(0.89)	55.96(.69)	59.95(0.94)	60.72(1.09)	61.37(0.87)	58.51(.56)
7	55.23(0.76)	54.01(.93)	50.65(1.00)	52.67(0.98)	54.68(0.90)	53.77(.71)
8	58.66(0.80)	54.26(.91)	63.88(0.86)	63.02(0.74)	66.33(0.74)	63.86(.83)

Appendix A10. Generation(Gen.) means and standard errors for feed efficiency(g/g) in each of the three environments for the adjusted feed efficiency(AFE) and Control lines.

	Environment					
	Corn		Rye		Wheat	
Line	AFE	Control	AFE	Control	AFE	Control
Gen.						
0	---	---	---	---	---	---
1	.227(.004)	.230(.005)	.204(.004)	.179(.006)	.237(.005)	.228(.005)
2	.281(.005)	.274(.005)	.235(.005)	.224(.005)	.242(.003)	.242(.004)
3	.260(.006)	.265(.004)	.224(.005)	.227(.005)	.218(.004)	.215(.004)
4	.249(.007)	.247(.005)	.212(.004)	.206(.003)	.216(.004)	.212(.002)
5	.231(.005)	.237(.004)	.208(.005)	.197(.003)	.202(.003)	.199(.003)
6	.241(.004)	.243(.004)	.224(.004)	.211(.003)	.231(.003)	.233(.002)
7	.258(.004)	.247(.006)	.205(.004)	.196(.004)	.232(.005)	.226(.003)
8	.222(.004)	.212(.004)	.198(.004)	.189(.004)	.201(.003)	.198(.003)

Appendix A11. Generation(Gen.) means and standard errors for adjusted body weight(g) in each of the three environments for the adjusted feed efficiency(AFE) and Control lines.

	Environment					
	Corn		Rye		Wheat	
Line Gen.	AFE	Control	AFE	Control	AFE	Control
0	---	---	---	---	---	---
1	23.51(.34)	23.00(.31)	21.74(.29)	19.85(.38)	22.99(.33)	21.63(.34)
2	24.00(.37)	23.86(.36)	22.29(.36)	21.75(.32)	23.25(.25)	22.77(.25)
3	22.70(.37)	22.25(.29)	21.75(.40)	20.86(.36)	21.23(.35)	20.52(.28)
4	22.33(.44)	21.37(.32)	22.10(.35)	21.40(.32)	23.78(.33)	22.98(.27)
5	23.91(.37)	23.68(.26)	22.91(.39)	22.09(.26)	23.13(.27)	22.09(.21)
6	24.58(.29)	23.97(.27)	23.35(.34)	22.70(.30)	24.06(.28)	22.98(.19)
7	24.42(.28)	23.65(.40)	20.46(.28)	20.36(.32)	22.54(.32)	22.10(.20)

Appendix A12. Generation(Gen.) means and standard errors for adjusted feed efficiency (g/g) in each of the three environments for the adjusted feed efficiency (AFE) and Control lines.

	Environment					
	Corn		Rye		Wheat	
Line Gen.	AFE	Control	AFE	Control	AFE	Control
0	---	---	---	---	---	---
1	.242(.004)	.240(.004)	.205(.004)	.184(.005)	.241(.004)	.229(.004)
2	.271(.005)	.270(.005)	.225(.005)	.220(.004)	.239(.003)	.236(.004)
3	.254(.005)	.253(.004)	.218(.005)	.216(.005)	.220(.004)	.214(.004)
4	.256(.006)	.254(.004)	.219(.004)	.208(.003)	.230(.004)	.223(.002)
5	.257(.005)	.261(.003)	.218(.005)	.211(.003)	.222(.003)	.211(.002)
6	.262(.003)	.262(.003)	.229(.004)	.219(.003)	.239(.003)	.227(.002)
7	.266(.003)	.259(.005)	.203(.004)	.196(.004)	.239(.005)	.227(.003)

Appendix B1. Analysis of variance of unadjusted traits in the Purina Control lines

Trait	Source	df	Type III sum of squares	F
Initial weight	Environment (E)	2	55.78	XX
	Generation (G)	7	1194.34	XX
	E x G	14	430.23	XX
	Residual	1163	3488.48	
Final weight	Environment (E)	2	5.18	N.S.
	Generation (G)	7	2549.13	XX
	E x G	14	589.80	XX
	Residual	1163	8646.78	
Feed intake	Environment (E)	2	166.48	N.S.
	Generation (G)	6	18575.45	XX
	E x G	12	9485.60	XX
	Residual	1017	44745.06	

XX $P<.01$

N.S. Not significant

Appendix B2. Analysis of variance of unadjusted traits in the Diet Control lines

Trait	Source	df	Type III sum of squares	F
Initial weight	Environment	2	33.77	XX
	Generation (G)	6	1223.50	XX
	Environment (E)	12	230.55	XX
	G x E	1008	2698.49	
Final weight	Environment	2	779.13	XX
	Generation	6	2324.99	XX
	E x G	12	798.09	XX
	Residual	1008	7456.53	
Feed intake	Environment	2	2341.01	XX
	Generation	6	15921.20	XX
	E x G	12	7984.79	XX
	Residual	1007	38892.03	

XX P<0.01

Appendix B3. Analysis of variance of litter size and conception rate

Trait	Source	df	Sum of squares	F
Litter size	Environment (E)	2	9.86	N.S.
	Generation (G)	16	650.21	XX
	E x G	12	224.27	XX
	Line (L)	3	3.09	N.S.
	E x L	6	70.80	X
	G x L	18	232.98	XX
	E x G x L	36	196.88	N.S.
	Residual	2432	12934.66	
Conception rate	Environment (E)	2	54.31	N.S.
	Generation (G)	6	161.48	N.S.
	E x G	12	373.02	X
	Line (L)	3	73.62	N.S.
	E x L	6	125.02	N.S.
	G x L	18	142.05	N.S.
	Residual	36	476.31	

X P<.05

XX P<.01

N.S. Not significant

Appendix B4. Analysis of variance of parameter (b) estimates for the corn, rye and wheat diets

Trait	Source	df	Sum of squares	F
Final weight	Environment (E)	2	1.45	XX
	Generation (G)	6	.30	N.S.
	Line (L)	2	.08	N.S.
	E x G	12	.52	N.S.
	E x L	4	.12	N.S.
	G x L	12	.41	N.S.
	Residual (ExGxL)	24	.77	
Feed intake	Environment (E)	2	8.38	XX
	Generation (G)	6	2.92	N.S.
	Line (L)	2	.09	N.S.
	E x G	12	4.89	N.S.
	E x L	4	.99	N.S.
	G x L	12	2.74	N.S.
	Residual (ExGxL)	24	8.42	
Feed efficiency	Environment (E)	2	2.63[1]	XX
	Generation (G)	6	.15	N.S.
	Line (L)	2	.16	N.S.
	E x G	12	1.02	N.S.
	E x L	4	.09	N.S.
	G x L	12	.89	N.S.
	Residual (ExGxL)	24	1.25	

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[1] Sum of squares x 10^4

XX P<.01

N.S. Not significant

Appendix B5. Analysis of variance of parameter (b) estimates for the Purina Control lines

Trait	Source	df	Sum of squares	F
Final weight	Environment (E)	2	.06	N.S.
	Generation (G)	6	.64	X
	Residual (ExG)	12	.29	
Feed intake	Environment (E)	2	.47	N.S.
	Generation (G)	6	4.36	N.S.
	Residual (ExG)	12	6.02	
Feed efficiency	Environment (E)	2	.22[1]	X
	Generation (G)	6	.64	X
	Residual (ExG)	12	.31	

[1] Sum of squares x 10^2

X P<.05

N.S. Not significant

Appendix B6. Nested analysis of variance of traits for the Purina Control lines

Trait	Source of variation	df	Mean squares	Variance component
Initial weight	Envigen[1]	20	71.41	
	Sire	139	6.07	.08
	Dam	337	5.28	2.33
	Residual	536	.53	.53
Final weight	Envigen	20	150.93	
	Sire	139	11.03	.05
	Dam	337	10.36	2.72
	Residual	536	4.83	4.83
Feed intake	Envigen	20	1411.80	
	Sire	139	61.87	.75
	Dam	337	55.56	12.46
	Residual	536	30.20	30.20
Feed efficiency	Envigen	20	24.38[2]	
	Sire	139	1.70	.05[3]
	Dam	337	1.36	.30
	Residual	536	.74	.74
ABW	Envigen	20	150.05	
	Sire	139	6.67	.16
	Dam	337	5.58	.71
	Residual	536	4.15	4.15
AFE	Envigen	20	24.87[2]	
	Sire	139	.96	.02[3]
	Dam	337	.84	.07
	Residual	536	.71	.71

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[1] Envigen - effect of each environment each generation.

[2] Mean square x 10^3.

[3] Variance component x 10^3.

Appendix B7. Nested analysis of variance of traits Pooled from the three lines (DC, ABW, AFE) and the three environments

Trait	Source of variation	df	Mean squares	Variance component
Initial weight	EGL[1]	62	85.17	
	Sire	426	5.49	.04
	Dam	1030	4.97	2.21
	Residual	1576	.55	.55
Final weight	EGL	62	213.34	
	Sire	426	13.62	.47
	Dam	1030	10.36	2.89
	Residual	1576	4.60	4.60
Feed intake	EGL	62	1434.12	
	Sire	426	59.25	1.97
	Dam	1030	46.11	7.52
	Residual	1576	31.10	31.10
Feed efficiency	EGL	62	23.33[2]	
	Sire	426	1.65	.05[3]
	Dam	1030	1.27	.31
	Residual	1576	.65	.65
ABW	EGL	62	69.01	
	Sire	426	7.07	.21
	Dam	1030	5.69	.78
	Residual	1576	4.14	4.14
AFE	EGL	62	22.41[2]	
	Sire	426	1.33	.62[3]
	Dam	1030	.97	.18
	Residual	1576	.61	.61

[1] EGL - effect of each environment, each generation, each line.

[2] Mean square x 10^3.

[3] Variance component x 10^3.

Appendix B8. Analysis of variance for realized heritability estimates for the ABW and AFE lines in each environment

Environment	Line	Mean square regression	Mean square residual	F
Corn	ABW	.88	.05	XX
	AFE[1]	.03	.15	N.S.
Rye	ABW	.14	.66	N.S.
	AFE[1]	.14	.10	N.S.
Wheat	ABW	.52	.38	N.S.
	AFE[1]	.65	.01	XX

[1] Mean square x 10^4.

XX P<.01

N.S. Not significant

Appendix B9. One-half cumulative selection differentials and responses in the ABW line for each of the three environments

	Environment					
	Corn		Rye		Wheat	
Gen.	Σ½ S.D.	ΣResponse	Σ½ S.D.	ΣResponse	Σ½ S.D.	ΣResponse
2	1.91	.12	2.09	.35	2.13	.41
3	3.21	.75	3.43	1.43	3.30	.54
4	4.48	.68	4.88	.71	4.57	1.29
5	5.77	.81	6.40	1.22	6.03	1.37
6	5.68	.99	7.95	.87	7.10	1.32
7	6.62	1.27	9.47	1.23	8.42	1.13

Appendix B10. One-half cumulative selection differentials and responses in the AFE line for each of the three environments

	Environment					
	Corn		Rye		Wheat	
Gen.	Σ½ S.D.	ΣResponse	Σ½ S.D.	ΣResponse	Σ½ S.D.	ΣResponse
1	.028	-	.022	-	.018	-
2	.046	.001	.033	.005	.033	.003
3	.065	.001	.055	.002	.046	.006
4	.083	.002	.074	.011	.063	.007
5	.100	-.004	.090	.007	.078	.011
6	.102	.000	.107	.010	.098	.012
7	.117	.007	.123	.007	.103	.012

Appendix B11. Analysis of variance for regression of all traits (as deviation from control) on generation number in the adjusted body weight line in each environment

Trait	Environment	Mean square regression	Mean square residual	F
Initial weight	Corn	.366	.346	N.S.
	Rye	.292	.200	N.S.
	Wheat	.270	.381	N.S.
Final weight	Corn	1.993	.315	N.S.
	Rye	.014	.191	N.S.
	Wheat	1.344	.327	N.S.
Feed intake	Corn	5.206	2.112	N.S.
	Rye	.501	.463	N.S.
	Wheat	4.701	.778	N.S.
Feed efficiency	Corn	$.42 \times 10^{-4}$	$.74 \times 10^{-4}$	N.S.
	Rye	$.01 \times 10^{-4}$	$.48 \times 10^{-4}$	N.S.
	Wheat	$.02 \times 10^{-4}$	1.44×10^{-4}	N.S.
Adjusted body weight	Corn*	.869	.056	X
	Rye	.555	.221	N.S.
	Wheat	.518	.095	N.S.
Adjusted feed efficiency	Corn*	1.34×10^{-4}	$.19 \times 10^{-4}$	X
	Rye	$.02 \times 10^{-4}$	$.59 \times 10^{-4}$	N.S.
	Wheat***	$.45 \times 10^{-4}$	$.03 \times 10^{-4}$	X

X $P<.05$

N.S. Not significant

Appendix B12. Analysis of variance for regression of all traits (as deviation from control) on generation number in the adjusted feed efficiency line for each environment

Trait	Environment	Mean square regression	Mean square residual	F
Initial weight	Corn	.0004	.241	N.S.
	Rye	.0124	.845	N.S.
	Wheat	.1651	.147	N.S.
Final weight	Corn	.128	.307	N.S.
	Rye	.214	1.334	N.S.
	Wheat	.344	.281	N.S.
Feed intake	Corn	1.361	1.708	N.S.
	Rye	8.421	5.878	N.S.
	Wheat	.267	1.905	N.S.
Feed efficiency	Corn	.06x10^{-4}	.56x10^{-4}	N.S.
	Rye	.26x10^{-4}	.36x10^{-4}	N.S.
	Wheat	.03x10^{-4}	.10x10^{-4}	N.S.
Adjusted body weight	Corn	.120	.094	N.S.
	Rye	.112	.071	N.S.
	Wheat	.540	.006	X
Adjusted feed efficiency	Corn	.06x10^{-4}	.14x10^{-4}	N.S.
	Rye	.13x10^{-4}	.11x10^{-4}	N.S.
	Wheat	.64x10^{-4}	.03x10^{-4}	XX

* $P<.05$

XX $P<.01$

N.S. Not significant

Appendix B13. Analysis of variance of digestibility between 21 and 28 days (Dig. 1), 28 and 35 days (Dig. 2) and 21 and 35 days (Dig. 3) estimated in generation seven

Trait	Source	df	Sum of squares	F
Dig 1	Environment (E)	2	.16	XX
	Line (L)	3	3.96	XX
	E x L	6	.01	X
	Residual	559	.51	
Dig. 2	Environment (E)	2	.01	X
	Line (L)	3	3.96	XX
	E x L	6	.03	X
	Residual	549	1.10	
Dig. 3	Environment (E)	2	.07	XX
	Line (L)	3	4.02	XX
	E x L	6	.01	XX
	Residual	549	.27	

X P<.05

XX P<.01

Appendix C1. Means and standard errors for traits in each diet and each line in the Corn Environment during the crossover study (generation 8)

	Diet		
	Corn	Rye	Wheat
A. Line - ABW			
Initial weight (g)	16.2(0.4)	15.4(0.3)	15.4(0.3)
Final weight (g)	28.6(0.5)	28.0(0.5)	27.2(0.4)
Feed intake (g)	57.7(1.2)	62.7(1.3)	59.0(1.5)
Feed efficiency (g/g)*	21.7(0.6)	20.0(0.4)	20.2(0.6)
Digestibility (%)			
Week 1	82.1(0.3)	78.1(0.4)	82.1(0.4)
Week 2	77.0(0.6)	74.5(0.4)	76.9(0.6)
Overall	79.7(0.4)	76.3(0.3)	79.6(0.5)
B. Line - AFE			
Initial weight (g)	13.7(0.3)	13.9(0.3)	14.0(0.4)
Final weight (g)	26.9(0.5)	26.3(0.5)	27.4(0.5)
Feed intake (g)	54.3(1.2)	60.6(1.5)	61.5(0.9)
Feed efficiency (g/g)	24.3(0.6)	20.2(0.6)	21.7(0.6)
Digestibility (%)			
Week 1	82.8(0.3)	78.7(0.6)	81.3(0.5)
Week 2	76.8(0.3)	74.6(0.5)	76.7(0.6)
Overall	80.0(0.2)	76.7(0.5)	79.1(0.4)
C. Line - Control			
Initial weight (g)	13.1(0.3)	13.6(0.3)	13.9(0.3)
Final weight (g)	24.6(0.6)	25.3(0.6)	25.0(0.4)
Feed intake (g)	49.0(1.5)	57.1(1.5)	56.7(1.2)
Feed efficiency (g/g)	23.5(0.7)	20.3(0.5)	19.8(0.6)
Digestibility (%)			
Week 1	84.4(0.4)	80.0(0.9)	81.8(1.3)
Week 2	78.0(0.4)	75.0(0.3)	77.0(0.8)
Overall	81.2(0.4)	77.5(0.5)	79.4(0.8)

*Feed efficienty (x 10^2)

Appendix C2. Means and standard errors for traits in each diet and each line in the Rye Environment during the crossover study (generation 8)

	Diet		
	Corn	Rye	Wheat
A. Line - ABW			
Initial weight (g)	17.1(0.3)	16.5(0.4)	16.1(0.3)
Final weight (g)	30.3(0.6)	29.1(0.6)	29.0(0.4)
Feed intake (g)	64.4(1.2)	68.9(1.4)	68.4(1.4)
Feed efficiency (g/g)*	20.4(0.5)	18.3(0.4)	18.7(0.4)
Digestibility (%)			
Week 1	81.4(0.4)	78.6(0.7)	80.5(0.8)
Week 2	77.5(0.4)	75.6(0.5)	78.1(0.4)
Overall	79.3(0.3)	77.0(0.4)	79.3(0.4)
B. Line - AFE			
Initial weight (g)	15.3(0.3)	15.3(0.4)	15.6(0.3)
Final weight (g)	28.5(0.5)	27.3(0.7)	28.1(0.7)
Feed intake (g)	60.5(1.4)	64.7(1.4)	66.6(1.4)
Feed efficiency (g/g)	21.8(0.5)	18.6(0.6)	18.9(0.7)
Digestibility (%)			
Week 1	82.2(0.3)	79.3(0.7)	82.8(0.6)
Week 2	77.9(0.4)	75.1(0.5)	78.6(0.5)
Overall	80.0(0.3)	77.1(0.5)	80.8(0.5)
C. Line - Control			
Initial weight (g)	14.5(0.4)	14.4(0.4)	14.9(0.5)
Final weight (g)	27.3(0.4)	26.2(0.5)	26.0(0.4)
Feed intake (g)	60.0(1.1)	65.2(0.9)	63.8(1.1)
Feed efficiency (g/g)	21.4(0.7)	18.1(0.4)	17.3(0.7)
Digestibility (%)			
Week 1	81.6(0.5)	77.6(0.6)	78.9(1.0)
Week 2	77.8(0.4)	74.7(0.4)	75.9(0.9)
Overall	79.6(0.4)	76.1(0.4)	77.4(1.0)

*Feed efficiency (x 10^2)

Appendix C3. Means and standard errors for traits in each diet and each line in the Wheat Environment during the crossover study (generation 8)

	Diet		
	Corn	Rye	Wheat
A. Line - ABW			
Initial weight (g)	15.9(0.3)	15.6(0.3)	15.9(0.3)
Final weight (g)	31.5(0.5)	30.1(0.1)	30.3(0.5)
Feed intake (g)	69.4(1.4)	72.4(1.2)	65.9(1.2)
Feed efficiency (g/g)*	22.5(0.6)	19.8(0.6)	21.9(0.6)
Digestibility (%)			
Week 1	81.6(0.6)	78.6(0.5)	76.4(0.5)
Week 2	76.6(0.3)	74.6(0.4)	72.8(0.4)
Overall	78.8(0.3)	76.4(0.4)	74.5(0.4)
B. Line - AFE			
Initial weight (g)	16.1(0.3)	15.7(0.5)	16.6(0.4)
Final weight (g)	30.1(0.3)	29.2(0.5)	28.9(0.4)
Feed intake (g)	63.8(0.8)	71.1(1.3)	64.5(1.1)
Feed efficiency (g/g)	22.0(0.5)	19.0(0.5)	19.2(0.5)
Digestibility (%)			
Week 1	81.8(0.4)	77.2(0.8)	76.1(0.4)
Week 2	78.0(0.3)	74.9(0.6)	73.0(0.6)
Overall	79.8(0.3)	76.0(0.6)	74.4(0.4)
C. Line - Control			
Initial weight (g)	15.0(0.3)	15.4(0.3)	14.7(0.4)
Final weight (g)	28.1(0.3)	27.5(0.5)	27.3(0.4)
Feed intake (g)	62.2(1.0)	69.2(1.4)	60.1(1.1)
Feed efficiency (g/g)	21.0(0.5)	17.6(0.5)	21.0(0.5)
Digestibility (%)			
Week 1	83.5(0.2)	77.5(1.0)	77.6(0.6)
Week 2	77.0(0.3)	74.4(0.5)	72.9(0.5)
Overall	80.1(0.2)	75.8(0.8)	75.0(0.4)

*Feed efficiency (x 10^2)

Appendix D1. Analysis of variance for the crossover study of traits (expressed as deviations from their own Diet Control) in the ABW line

Trait	Source	df	Sum of squares	F
Initial weight	Environment (E)	2	71.9	XX
	Diet (D)	2	35.9	XX
	E x D	4	27.2	X
	Residual	190	458.2	
Final weight	Environment (E)	2	.1	N.S.
	Diet (D)	2	29.2	N.S.
	E x D	4	22.2	N.S.
	Residual	190	1120.4	
Feed intake	Environment (E)	2	66.7	N.S.
	Diet (D)	2	289.6	X
	E x D	4	356.9	N.S.
	Residual	190	7260.1	
Feed efficiency	Environment (E)	2	1.5[1]	XX
	Diet (D)	2	0.6	XX
	E x D	4	0.7	X
	Residual	190	10.6	

[1] Sum of squares x 10^2

X P<.05

XX P<.01

N.S. Not significant

Appendix D2. Analysis of variance for the crossover study of traits (expressed as deviations from their own Diet Control) in the AFE line

Trait	Source	df	Sum of squares	F
Initial weight	Environment (E)	2	18.9	X
	Diet (D)	2	6.2	N.S.
	E x D	4	20.8	N.S.
	Residual	190	507.2	
Final weight	Environment (E)	2	5.8	N.S.
	Diet (D)	2	22.1	N.S.
	E x D	4	23.3	N.S.
	Residual	190	1078.6	
Feed intake	Environment (E)	2	427.4	XX
	Diet (D)	2	186.4	N.S.
	E x D	4	82.8	N.S.
	Residual	188	6301.3	
Feed efficiency	Environment (E)	2	2.1[1]	N.S.
	Diet (D)	2	.1	N.S.
	E x D	4	18.2	XX
	Residual	188	135.8	

[1] Sum of squares x 10^3

X P<.05

XX P<.01

N.S. Not significant

Appendix E. Photographs and dimensions of individual feeder cages

The outside dimensions of the plexiglass cages were twelve cm (height) by ten cm (width). A wire mesh floor was supported six cm from the top. The plexiglass tunnel feeder extending out from the centre of one of the four sides, one-half cm above the wire mesh floor, was ten cm long with a height and width of three cm. Wire mesh tubes, ten cm in length had a hole (approximately 2 cm square) at the bottom distal end. These tubes were inserted into each of the tunnel feeders and the hole provided excess to feed. The feed was held by metal containers which slid over the plexiglass tunnel.

NOTICE/AVIS

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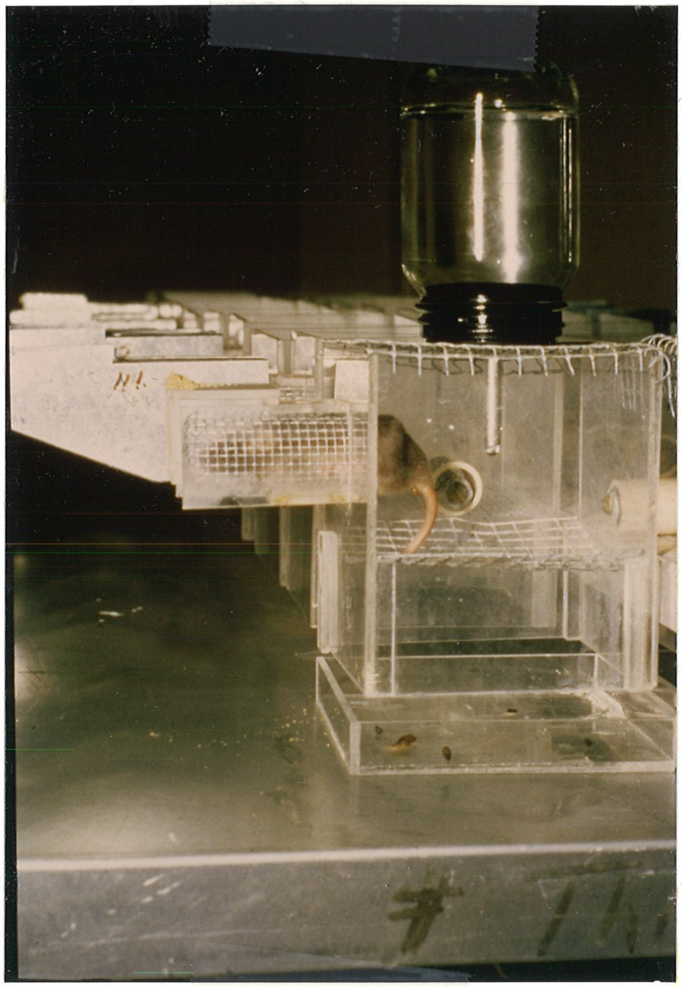
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