SELECTION FOR FEED CONVERSION EFFICIENCY IN THE LABORATORY MOUSE (*Mus musculus* L.)

by

Muhammad Aslam Bhatti

A Thesis

Submitted to

The University of Manitoba

in Partial Fulfillment of the Requirements

for the Degree of

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MUHAMMAD ASLAM BHATTI

A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

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ABSTRACT

Recurrent mass selection for feed conversion efficiency (FCE) in mice was practiced for six generations in two lines fed ad libitum (AL) and two lines restricted to 80% of ad libitum (R). A random breeding control line (C), also fed ad libitum was maintained throughout the study. In one line of each pair of selected lines the test period was terminated after a fixed time (14 days) (i.e. TAL and TR) and after consumption of a fixed quantity of feed in the second line of the pair (i.e. WAL and WR). The fixed quantity of feed was the average ad libitum consumption of mice in the C line. Direct and correlated responses were evaluated. The correlated traits measured were initial weight, final weight, weight gain (G), feed consumption, carcass composition and litter size. Data were obtained from 300 mice per generation.

A significant ($P<.05$) direct response was found in the TR and WR lines; regression of response on generation number being -1.36 ± 0.31 and -1.09 ± 0.39 respectively. There was a significant ($P<.05$) decrease in initial weight on test in the TR and WAL lines. No significant change was observed in any other correlated trait. In the lines which became lighter in initial weight (TR, WAL) mature body weight was significantly lower ($P<.05$) than in the C line when measured in the sixth generation. The heritability estimates of FCE were higher in the restricted lines (0.31 ± 0.12 for TR and 0.37 ± 0.29 for WR) as compared to ad libitum lines (0.13 ± 0.20 for TAL and 0.13 ± 0.25 for WAL). The heritability of FCE was 0.17 ± 0.31 in the C line. Phenotypic and genetic correlations between FCE and G were high and negative in all lines. Progeny from each line were tested in each of the other feeding regimes each generation to measure line x feeding regime interaction. This interaction was statistically significant ($P<0.01$).

The magnitude of the heritability estimates obtained in the TR and WR lines indicate that there is a higher proportion of genetic variation in efficiency of feed conversion in these lines. It was concluded that selection for FCE was most effective under restricted feeding.

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INTRODUCTION

Since feed costs account for a large part of production costs, feed conversion efficiency (FCE) is one of the most important traits to consider in livestock improvement. Moderately high heritability estimates have been obtained for FCE by many workers (Craft, 1958; Thomas et al., 1958a; Warwick, 1958; Wilson, 1969; Sutherland et al., 1970) which suggest that this trait should respond favourably to selection. However, little direct selection has been applied mainly because of the difficulties of measuring FCE in individual animals.

A high genetic correlation between weight gain (G) or body weight and feed efficiency has been reported for a number of species (Koch et al., 1963, in cattle; Robison and Berruecos, 1973b, in swine; Wilson, 1969, in chickens; and Sutherland et al., 1970, in mice). Because of this high genetic relationship, improvement in FCE has usually been brought about as a correlated response to selection for G. But differences between genetic stocks in G and FCE may simply be due to differences in appetite (Siegel and Wisman, 1966). A similar explanation has been proposed by Timon and Eisen (1970). Proudman et al., (1970) found no difference in FCE in chickens selected for high G whether they were fed ad libitum or restricted. Selection for rapid growth per se may not necessarily be the best selection criterion for increasing FCE because of an accompanying increase in feed consumption (Eisen, 1974; Sutherland et al., 1974). Direct selection for FCE could be an alternative.

This experiment was conducted to study the effect of selection for FCE in ad libitum or restricted feeding regimes and to study the effect of terminating the test period either after a fixed time or after consumption of a fixed quantity of feed in each regime.

Correlated genetic changes in initial weight, final weight, G, feed consumption, litter size and carcass traits resulting from selection of mice for FCE were also of interest. Heritabilities of FCE and G and phenotypic and genetic correlations between these two traits were estimated. A crossover study and the theoretical comparison of indirect selection to direct selection were included in this investigation.

REVIEW OF LITERATURE

Differences in efficiency of feed utilization have long been recognized in mice and rats but less emphasis has been given to this trait in livestock or poultry. Recently, due to the world shortage of both plant and animal proteins, and consequently high feed costs, the necessity to improve the efficiency of feed utilization has become more urgent. Feed costs are relatively higher in poultry and swine. This has led to more research in these species than in cattle or sheep. In this section the different species will be considered separately.

1. Mice

a) Responses to selection for growth rate, appetite and feed efficiency.

Fowler (1962) reported that during the course of selection for large or small body size, mice of the large line consumed more feed and utilized it more efficiently during the period of most rapid growth than did mice of the small line. It was suggested that the efficiency with which the feed was utilized could be modified by selection; changes in feed efficiency and appetite were positively correlated with changes in growth rate. He further added, that the increased efficiency of large mice was not entirely associated with a greater proportion of the ingested feed being absorbed from the gut. Large mice absorbed a greater proportion of protein, though the difference was not sufficient to account for the large weight difference between the large and small lines.

Sutherland et al. (1970) reported on four lines of mice that were created from F_2's of highly inbred lines. One of the lines was maintained as a control line. In the other three lines an initial nine generations of mass selection entirely for rate of gain between 4 and 11 weeks of age was accompanied by a marked increase in rate of gain, a moderate increase in feed intake and therefore a marked increase in gross efficiency. Selection was modified at generation 9. During the next 12 generations line 1 of the three mass selection lines was selected for efficiency of feed use, line 2 was selected for feed intake, and line 3 was selected for rate of gain as in the previous generation. After the selection scheme was modified, rate of gain continued to increase in all three selected lines with the most rapid gain occurring in fact, in line 1, which was selected for efficiency. Regressions of mean weight gain on generation number for generations 10 to 21 were respectively, .75±.113, .40±.100 and .38±.115 grams, the lowest being the line selected for rate of gain. Feed intake continued to increase in all lines. The regressions of mean feed consumption on generation number were 1.99±.936, 3.11±.708 and 1.50±.918 grams, respectively for lines 1, 2 and 3. Gross efficiency, or grams gain per gram feed intake likewise improved; regressions being between .0031±.00067, .0006±.00057 and .0013±.00052 g/g per generation respectively.

Timon and Eisen (1970) compared growth rate, feed consumption and feed efficiency in mice selected for increased postweaning weight gain (High line) and Control line mice under ad libitum and restricted feeding conditions. Data based on 199 mice recorded over the postweaning growth period 21-57 days were analyzed to show the pattern of change and total change in these traits as a result of selection for postweaning weight gain. The results showed that High mice consumed more feed, grew at a more rapid rate and were more efficient than the unselected Controls.

The High mice had a larger appetite as measured by feed consumed per gram body weight.

It was concluded that the most important change as a result of nine generations of selection for postweaning gain was an increase in appetite which in turn resulted in increased growth rate and increased gross efficiency.

Sutherland et al. (1974) concluded that in tissue growth there seemed to be relatively little variation in energetic or net efficiency among animals. Increases in gross efficiency could be the result of increased capacity to ingest nutrients; the increased intake could virtually all be utilized for tissue growth since basic maintenance requirements are already met. When total gain was expressed as a ratio to total feed intake the gross efficiency appeared to have been markedly improved. It was also concluded that both growth rate and appetite were under genetic control and were rather highly correlated. Selection for increased growth rate was effective and was mandatorily accompanied by increased appetite, which resulted in improved gross efficiency but no change in net efficiency of tissue growth. Selection for appetite, on the other hand, was less effective in changing growth rate and resulted in somewhat lower gross efficiency but presumably also did not change net efficiency of tissue growth.

Brown and Frahm (1975) measured average daily feed consumption (ADFC) and feed efficiency (FE, gain/feed) from 21 to 42 days of age in three groups of mice during generation 11 to 14 of a study designed to measure responses to selection for increased growth. One group was selected for increased 21-day weight (WWL), a second for rapid gain between 21 and 42 days of age (ADGL) and the third group served as an unselected control (CL). Comparisons of FE and ADFC among WWL, ADGL and CL were very consistent over the four generations studied. As a result of the selection pressure applied WWL and ADGL exceeded (P<.001) CL in 21-day weight by an average of 26.4% and 17.2% respectively and in 21 to 42-day ADG by 14.1% and 53.1%, respectively. The WWL and ADGL exceeded (P<.001) CL in ADFC by 17.4% and 26.9% respectively. There was a 21.6% improvement (P<.001) in FE in ADGL over CL; however, WWL were 2.4% (P<.05) less efficient than CL.

Eisen (1977) constructed a bidirectional restricted selection index to maximize genetic change in postweaning weight gain from 3 to 6 weeks of age, while limiting genetic response in feed intake to zero. Correlated responses in postweaning gain were significant (P<.01) in the intended direction of selection in both lines, but feed intake did not respond significantly. Little net change occurred in feed intake until genetic change in postweaning gain had reached about one phenotype standard deviation. Subsequently, genetic change in feed intake tended to follow the direction of response in postweaning gain, but this was not significant. Feed efficiency showed marked correlated responses while 3-week body weight did not respond to the restricted index selection.

Basic to an understanding of the genetics of growth, appetite and feed utilization is a knowledge of the effect selection for these traits has on body composition. Fowler (1958) found that selection for increased six-week body weight in mice increased rate of fat deposition whereas selection for low six-week weight reduced the proportion of fat in the carcass.

Biondini et al (1968) examined the body composition of mice selected for rapid growth rate. Chemical composition of whole carcass of mice from three replicate lines selected for rapid growth and from an unselected control line was determined each generation for 10 generations. Traits studied included gain on test, feed consumed on test, live weight at sacrifice and grams of each of the following: ether extract, moisture, crude protein, and ash. Within line regression analysis showed rate of gain increased significantly over generations in all lines; that the amount of all carcass components increased in the selected lines; and that ether extract increased proportionally much more in two of the lines than did the other components. In the third selected line increases in ether extract and ash were nonsignificant while proportional changes were all nonsignificant ($P \leq .05$). The control line displayed a highly significant decrease in ether extract.

Lang and Legates (1969) characterized mice selected for high (H_6) and low (L_6) 6-week body weight and a randombred control population (C_1) for composition of growth. Individual body weights were obtained from birth to 8 weeks of age on 682 mice representative of the three lines. Individual whole carcass determinations of water, fat, ash and protein (residual) were obtained for 180 mice sampled weekly from 3-8 weeks of age. The composition of growth yielded no evidence that the more rapid growth rate in the H_6 line resulted from an increase in fat deposition relative to the other carcass components. Percentage water was highly correlated negatively with percentage fat. Percentages protein and ash were essentially constant across lines and ages.

Timon et al. (1970) compared carcass composition of mice selected for nine generations for rapid postweaning gain (High line) with randombred mice (Control line) under both ad libitum and restricted feed intake. The data, based on 196 mice, consisted of water, protein, ether extract and ash determinations on the skinned and eviscerated carcasses at 57 days of age. Weights of water, protein, ether extract and ash increased as a result of selection and also were greater in males than in females. When weights of the components were expressed as a percentage of total carcass weight, the only differences between the two lines were that the ether extract increased and water decreased in the High line as compared to the Control line. There were no significant differences between the restricted and ad libitum fed mice in percent composition of any of the carcass components measured.

Sutherland et al. (1974) compared carcass composition of mice selected for 42 generations for high appetite with randombred control mice. The appetite line showed a higher percentage of fat and a slightly lower percentage of all other components; males and females, were 7% and 15% respectively fatter than the control line at 49 days of age.

Eisen (1976) reviewed results of growth curve analysis in mice and rats and reported that selection for postweaning growth rate of mice led to changes in the overall weights of all body components. Percent body fat increased in several lines selected for rapid postweaning gain, body weight or appetite. In contrast to changes in percent fat, percent protein remained remarkably stable.

The net conclusion, from these studies is that selection for increased body weight increases appetite and gross efficiency. (Fowler 1962; Sutherland et al. 1970; Timon and Eisen 1970; Sutherland et al.

1974). More feed intake by efficient mice in turn results in more fat deposition (Fowler 1958; Biondini et al. 1968; Timon et al. 1970; Eisen 1976). The findings of Lang and Legates (1969) are exceptions to other results. They do not indicate any change in body composition of mice as a correlated response to selection for growth rate. Selection for appetite is positively correlated with growth rate and fat deposition (Sutherland et al. 1970; Sutherland et al. 1974).

b) Heritabilities and genetic and phenotypic correlations.

Rahnefeld et al. (1965) estimated the additive genetic covariance and genetic correlation of postweaning gain and feed per unit gain for a genetically variable population of mice during a 17 generation span in which selection for postweaning gain was practiced. These estimates indicated a high (nearly perfect) negative genetic correlation.

Sutherland (1965) presented formulae for the prediction of the correlation between a ratio and its denominator in terms of the correlation between the numerator and the denominator and of the coefficient of variation of these two variables. To demonstrate the practical significance of the theory developed in this paper concerning the relationship between rate of gain and feed efficiency (total feed consumed/total gain on test) he used the results obtained in eight generations of selection for gain in body weight in mice. The gaining ability of some 200 male and 200 female mice per generation was tested between the ages of four weeks and 11 weeks. Using the formulae presented, both the phenotypic and genetic correlations between gain and feed efficiency (feed/gain) were predicted, and these values were compared with the correlation actually obtained from the data. There was reasonable agreement between predicted and actual values.

Sutherland *et al*. (1970) analyzed the results of 21 generations of selection in three lines of mice. The selection procedure in these lines has been outlined previously in this review. They obtained realized heritability estimates of .23$\pm$.020 over 21 generations in line 3, .29$\pm$.034 over the first nine generations in line 2 and .22$\pm$.067 over the first nine generations in line 1, for growth rate. Realized heritability from generation 10 through 21 for feed efficiency in line 1 and for feed intake in line 2 were .17$\pm$.042 and .20$\pm$.057 respectively. The realized genetic correlations among the three characters, rate of gain (G), feed intake (F) and efficiency (E) were as follows:

$$r_{A(GF)} = 0.71 \quad r_{A(GE)} = 0.91 \quad r_{A(EF)} = 0.36.$$

Jara-Almonte and White (1973) formed 57 paternal half-sib families (including 533 lactating female progeny) over three replicates in order to estimate heritabilities and genetic correlations among milk production, feed intake, body weight gain and the efficiency of feed utilization. A nested model was used to estimate these parameters. The heritability values for gain in weight ranged from 0.12$\pm$.10 to 0.22$\pm$.12; for feed intake from 0.14$\pm$.11 to 0.34$\pm$.13; and for feed efficiency from 0.11$\pm$.10 to 0.24$\pm$.12. For the postweaning period from 21 to 42 days the genetic correlation between gain and feed efficiency was 0.75$\pm$.28. Genetic correlation between milk yield and postweaning gain was also large and positive.

Brown and Frahm (1975) obtained the estimates of the genetic parameters from half-sib estimates from the analysis of 203 male progeny. The heritability value for 21 to 42-day ADG was 1.20±.38; for ADFC was .73±.37; and for FE was 1.09±.38. The genetic correlations of 21 to 42-day ADG with ADFC and FE were estimated to be .55±.18 and .63±.16 respectively. This estimate between ADFC and FE was -.31±.32.

Eisen (1977) obtained heritabilities and genetic and phenotypic correlations from a paternal half-sib variance-covariance analysis. The estimates of heritability of postweaning gain, feed intake, and feed efficiency (from 3 to 6 weeks of age) were .24±.12, .47±.18, and .13±.07 respectively. The genetic correlations between postweaning gain and feed efficiency, postweaning gain and feed intake and feed intake and feed efficiency were .48±.28, .61±.19 and -.41±.27 respectively. Corresponding phenotypic values between these traits were .80, .47 and -.13 respectively.

It seems that growth rate and feed efficiency are highly correlated genetically (Rahnefeld _et al_. 1965; Sutherland 1965; Sutherland _et al_. 1970; Jara-Almonte and White 1973; Brown and Frahm 1975). The genetic correlations between feed consumption and growth rate are high (Sutherland _et al_. 1970, 0.71; Brown and Frahm 1975, 0.55). Whereas the genetic relationship between feed consumption and feed efficiency is low (Sutherland _et al_. 1970, 0.36; Brown and Frahm 1975, -0.31). This suggests that selection for feed consumption may not improve feed efficiency. The heritability values for growth rate and feed efficiency range from 0.12 to 1.20 and 0.11 to 1.09 respectively.

In almost all of the above studies feed efficiency has been measured as a correlated response from experiments conducted for direct selection in growth rate. The high correlation between gain in weight and feed efficiency resulted in the practice of substituting gain for feed efficiency. Feed efficiency is a ratio between two direct measurements, gain and feed intake. Some workers used gain/feed, others have used its reciprocal. After comparing different approaches to measure efficiency Sutherland (1965) has recommended the ratio of feed to gain.

Most of the studies have been carried out under ad libitum feeding but growth rate on a low plane of nutrition may be principally a matter of efficiency of feed utilization whereas on a high plane of nutrition it may be principally a matter of appetite (Falconer 1960). Moreover, selection for rapid growth per se may not necessarily be the ideal selection criterion for increasing efficiency of feed utilization because of an accompanying increase in feed consumption (Eisen 1977). It is therefore important to consider direct selection for feed efficiency in different feeding environments.

c) Genotype-environment interactions.

A controversial question among animal breeders has been the choice of the environmental conditions under which to practice selection. There were two schools of thought. One point of view was supported by the findings of Hammond (1947) that an environment favourable to the expression of the desired character will allow more rapid progress under selection and unfavourable environmental conditions tend to limit the response to selection. Thus if animals selected under favourable conditions are shifted to less favourable conditions they will express a higher level of performance than would have been attained by equal selection pressure under the less favourable environment. The second school of thought, which is now believed to be more valid holds that performance in a favourable environment is dependent upon a different genetic basis than performance in a less favourable environment. Thus animals should be selected in the environment under which they are expected to perform. This point of view was supported by the work of Falconer and Latyszewski (1952) in which mice were selected for six-week weight under high and low planes of nutrition. Weight increased under selection in both groups. Exchanges in nutritional level were made after several generations. Mice selected on a restricted diet and placed on unlimited feeding were just as heavy as those selected on the full diet. On the other hand, mice selected on the full diet and raised on the restricted diet showed no improvement over the unselected level. It appeared that two different characters were selected. Mice on full feed were selected for high appetite, and mice on restricted feed were selected for efficiency of feed utilization. Falconer (1952) reported that the genetic situation explaining the above results is that of a genotype-environment interaction. He suggested that when a single trait exhibited a genotype-environment interaction under two environments, it should be considered as two separate traits. Lush (1945), Kelley (1949), Morely (1956) and Fowler and Ensminger (1960) were of the same opinion.

2. Rats

The earliest study of feed efficiency with rats appears to be that of Morris et al. (1933) who developed from the progeny of a single pair of somewhat related rats, in nine generations, two strains differing in feed utilization efficiency. The low strain was approximately 40 percent less efficient than the high efficiency strain.

Palmer et al. (1946) determined the energy requirement for maintenance for 47 high efficiency strain male rats and 43 low efficiency strain male rats. The low efficiency strain had a significantly higher maintenance requirement. They further reported that the less efficient strain animals consumed less dry matter and grew at a slower rate. The high efficiency strain rats had a higher percentage of ether extract and a lower percentage of protein than did the low efficiency strain rats.

Park et al. (1966) conducted a selection experiment to determine the degree of dietary restriction in feed intake and the amount of protein to use. Groups of rats of both sexes were reared on (1) ad libitum feeding of a standard diet (full feed, FF), (2) 3/4 restriction in feed intake of the standard diet (low feeding, LF), (3) ad libitum feeding of diets in which the total protein content was restricted (low protein, LP) for the period from 3 to 9 weeks of age. Selection was on the basis of individual postweaning gains during the test period. Seventeen generations of selection were completed. Realized heritability and absolute response to selection were larger under a full feeding regime than under a limited feeding regime, but when the FF line was put on the LF regime, the response was significantly smaller than that on the FF regime. The interaction between line and feeding regime for postweaning gain from 3 to 9 weeks of age was significant over all generations, but failed to reach statistical significance in the majority of individual generations where numbers of animals tested were small.

Chapman (1973) with reference to the selection experiment reported by Park et al. (1966) stated that after 16 generations of selection for gain, with a realized heritability of 0.11 in the full fed group, selection was relaxed until the 27th generation. The full-fed stock lost about half of its superiority over the control population by generation 22 and half of the remainder by generation 27.

3. Poultry

Hammond and Bird (1942) studied the variability of growth in chickens. They divided 50 chicks into two groups, one of which included all chicks that exceeded 118 grams, while the other included those weighing less than 118 grams at three weeks of age. They concluded that on the basis of liveweight, the fast growing group was more than twice as efficient as the slow growing group in the utilization of feed at six weeks of age.

Glazener and Jull (1946) studied efficiency of feed utilization in two strains of New Hampshires and Barred Plymouth Rocks and found that the progeny of the long-shanked strains tended to grow faster and utilized feed more efficiently than the progeny of the short-shanked strains. Hess and Jull (1948) reported that the strain of New Hampshires was more efficient in utilizing feed than the strain of Barred Plymouth Rocks.

Fox and Bohren (1954) studied individual feed efficiency (gain/feed) and growth in four breeds of chickens from four to ten weeks of