SELECTION RESULTS FOR EFFICIENCY OF FOOD UTILISATION IN LIVESTOCK AND POULTRY

Selección para la eficiencia de la utilización de los alimentos en ganadería y avicultura

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INTRODUCTION

It has been recognised for many years that food conversion efficiency is a major determinant of profitability in intensive livestock production. Notwithstanding this, there has been little direct selection for feed efficiency practised by commercial breeders and genetic improvement in this trait has been obtained in most species as a correlated response to selection for increased liveweight gain. There are a number of reasons for this: It is considerably simpler and less costly to weight animals than to measure individual food consumption over a given period; where animals are grown to a given weight, more rapid growth means less food required per unit of gain since maintenance requirements are lower due to the shorter growing period; and the heritability of weight gain is in most cases moderate to high allowing good response to selection. Indeed, selection for increased juvenile body weight in broiler chickens over the past 30 years or so has resulted in a dramatic improvement in food conversion efficiency to market weight.

Selection for weight gain, however, is often associated with certain undesirable correlated responses such as larger mature size, a depression in reproductive performance and an increase in the proportion of fat in the carcass. Furthermore there is increasing evidence from selection studies in some species to suggest that variation in feed efficiency independent of body weight gain is sufficiently large to consider the possibility of direct selection for this trait. These considerations argue a case for careful reappraisal of past selection practices.

FEED EFFICIENCY DEFINED

Prior to any discussion of feed efficiency, a clear definition of the different methods of expressing efficiency is required since such measures may have quite different properties. At the outset a distinction between feed efficiency and energetic efficiency should be made. Energetic efficiency as defined by Brody (1945) is "the ratio of the desired form of output energy to the given form of input energy" whereas feed efficiency for growth usually refers to the weight ratio of body weight gain : food consumption both expressed in the same units and does not take account of the energy content of the feed or gain. This form of expression or its reciprocal are actually measures of gross efficiency, i.e. include both a maintenance and growth component. The measure feed/gain is usually referred to as the food conversion ratio (FCR). Efficiency can also be measured over different intervals, viz., age to age, weight to weight or age to weight. Measurement of efficiency on a weight to weight or age to weight basis favours faster growing animals since maintenance requirements are reduced with the shorter growing period whereas these animals are penalised in age to age measurement in that they carry a heavier weight with its higher maintenance cost for the age constant period.

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A number of workers have looked at the relative merits of the different methods of expressing feed efficiency. Koch et al. (1963) advocated abandoning the ratio technique of determining feed efficiency on the grounds that the ratio is a biased estimate. They suggested three other methods for measuring feed efficiency:

(i) average daily gain adjusted for corrected food consumption (corrected for midweight)
(ii) average daily food consumption adjusted for daily gain and midweight and
(iii) the ratio of gain/food consumption, with food consumption adjusted for midweight.

In comparisons of unadjusted feed/gain and gain/feed, Timon and Eisen (1970) in a study with mice concluded that since the coefficient of variation of feed/gain was considerably larger than that for gain/feed (79.9% of 23.7%), gain/feed would be the preferred measure of efficiency where comparisons were made over a constant age interval. Contrary conclusions were reached by Robison and Berruecos (1973) using swine data. They suggested that feed/gain provides a better estimate of feed efficiency than gain/feed for both age to age and weight to weight intervals. It should be pointed out that whilst the measures of feed/gain and gain/feed have different mathematical properties resulting in different statistical estimates of heritabilities and coefficients of variation, irrespective of the measure used and given the same measurement interval, the same animals would be selected in a single trait selection programme for improved feed efficiency.

Conflicting recommendations have been made as to the desirability of age to age or weight to weight measurement intervals in evaluating differences in feed efficiency in pigs and mice, with Nordskog et al. (1944) and Biswas et al. (1966) advocating the former and Park (1965), Timon and Eisen (1970) and Robison and Berruecos (1973) advocating the latter. Where animals are marketed at predetermined weights, it is obviously desirable to compare their performance in terms of food conversion efficiency and carcass composition at those weights. Practical considerations would suggest, however, that where direct selection for feed efficiency is contemplated in commercial breeding programmes involving large numbers of individuals, e.g. broilers, measurements based on weight to weight or age to weight intervals pose considerable problems. Where fewer animals are under test, e.g. pigs or cattle, there is greater opportunity for measurement of feed efficiency over weight constant or age to weight intervals.

COMPONENTS OF FEED EFFICIENCY

Genetic improvement in gross efficiency measured as the weight ratio of gain/feed can presumably be achieved by one or more of the following effects:

i) a reduction in external losses, i.e. spillage as affected by feeding behaviour
ii) an increase in the digestibility/metabolisability of dietary nutrients
iii) an increase in food intake allowing more food to be used for gain and proportionately less for maintenance
iv) a reduction in maintenance energy requirements
v) an increase in the availability of metabolisable energy (ME) for gain

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vi) a reduction in the energy content of the gain, i.e. partitioning of water, fat and protein in the body.

The latter point highlights the difference between the weight ratio measure of gross efficiency and measures of energetic efficiency.

Considering these effects in turn -

i) External losses can be controlled by the use of well designed and managed feeders.

ii) It is generally held that there is little variation in digestibility or metabolisability of nutrients between different strains or breeds (Fowler 1962, Blaxter 1968, Sutherland et al. 1974). There have been, however, reports of differences in metabolisability of dietary energy between strains and breeds of chickens (e.g. Sibbald and Slinger 1963), and between lines of chickens selected for divergent 8-week body weight (Proudman et al. 1970) or for efficiency and its component traits (Pym and Farrell 1977). The latter results indicated that metabolisability could be improved by selection for improved food conversion efficiency.

iii) A number of studies (Fowler 1962, Timon and Eisen 1970, Sutherland et al. 1974) have suggested that in selection for increased weight gain, the improved gross efficiency observed is directly attributable to increased intake resulting in a spreading of the maintenance requirement and that there is no improvement in the net efficiency of growth.

iv) Studies with mice and chickens have yielded conflicting information on the effects of selection for growth and efficiency upon maintenance energy requirements. Since maintenance requirements are complex and affected by a large number of factors which can themselves vary widely, e.g. activity, body composition, insulation to heat loss, it is reasonable to expect there to be the potential for significant differences in maintenance requirements between lines selected for feed efficiency and its components.

v) Since fat is deposited with a much greater energetic efficiency than protein (75% of 44% in rats, Pullar and Webster 1977; 89% of 65% in chickens, Pym and Farrell 1977), it is energetically more efficient to deposit fat. However because of the higher energy density of fat compared to protein (39 of 23 kJ/g), on a dry weight basis the two are deposited with roughly the same energy cost.

vi) Since protein is associated with about 70% water in muscle tissue and fat with only about 10% water in fatty tissue, and since the two are deposited gram for gram with the same approximate energy cost, it should in theory cost about three times as much energetically to deposit the same weight of fatty tissue as muscle.

Factors v) and vi) tend to be antagonistic. Any improvement in energetic efficiency associated with increased fat deposition will possibly result in a decrease in gross efficiency.

EXPERIMENTS PROVIDING INFORMATION ON FEED EFFICIENCY

Broadly speaking there are about five types of experiments which have provided information on the genetic and physiological associations of growth, appetite and feed efficiency. These can be categorised as follows:
a) within breed or strain genetic or phenotypic comparisons
b) between breed comparisons
c) selection experiments for weight gain in which feed efficiency was measured as a correlated trait
d) selection experiments for weight gain under restricted feeding
e) selection experiments for feed efficiency per se.

a) Parent offspring or sib analyses give predictive information on one generation of divergent selection. No estimate of asymmetry in direct or correlated response is obtainable from such analyses and changes in heritability and the genetic correlation as selection proceeds are also not taken into account. Nevertheless such analyses have fulfilled a useful function in providing an estimate of the inheritance and general association between feed efficiency and its component traits.

b) Here genetic differences are generally complex and may be attributable to selection for different trait combinations in the different breeds. As such, relationships between feed efficiency, growth and body composition must be interpreted with caution.

c) Much of the earlier information on feed efficiency in mice was obtained from this type of experiment. Correlated response in feed efficiency was measured in lines selected for high or low weight gain over various intervals and inferences made as to the relative effectiveness of improving feed efficiency by direct or indirect means.

d) There are a number of pig and mouse selection experiments in which animals have been selected for increased growth rate under restricted feeding in an endeavour to ascertain if efficiency can be improved by directing more metabolisable energy towards protein and less towards fat synthesis. Keilanowski (1968) proposed this as a means of improving the efficiency of lean tissue growth in pigs.

e) A number of selection experiments have now been conducted with pigs, chickens, rats and mice in which some measure of feed efficiency has been used as a selection criterion. Measures of efficiency used in the different experiments have ranged from gain/feed, growth on a fixed amount of feed (on a continuous, not daily, basis) to a restricted selection index.

Within and between strain or breed studies

A good review of genetic aspects of feed efficiency in some farm and laboratory animals has been provided by Yuksel (1979). In that review, within and between strain and breed comparisons are well covered and it is not intended to discuss these results here. The majority of information on cattle comes from this type of study. As indicated by the title, this paper will deal principally with results from selection experiments in which feed utilisation efficiency was either a selected or correlated trait.

Selection for growth rate

There is a large body of published research work, particularly with mice,
which describes correlated response in feed efficiency and body composition to selection for high or low body weight gain under *ad libitum* feeding. Studies with mice (Fowler 1962, Rahmefeld *et al.* 1965, Lang and Legates 1969, Timon and Eisen 1970, Sutherland *et al.* 1970, Jara-Almonte and White 1973, Bakker 1974, Brown and Frahm 1975, Canolty and Koong 1976, and Eisen *et al.* 1977), chickens (Lepore 1965, Siegel and Wisman 1966, and Proudman *et al.* 1970) and quail (Marks 1980) have generally shown positive correlated response in both food consumption and feed efficiency to selection for increased liveweight gain, whether measured over age constant or weight constant periods. The primary effect of selection for gain would appear to be to increase the capacity to ingest nutrients which can largely be used for tissue growth since maintenance requirements are already met. Gross feed efficiency expressed as a ratio of gain to food consumption will thus automatically improve. Timon and Eisen (1970) in an exhaustive study of correlated response in feed efficiency to selection for growth rate in mice compared the efficiency of high weight gain and control line animals over age constant and weight constant periods under *ad libitum* and restricted feeding.

Over a weight constant period between 15 and 25 g the high line was considerably more efficient but when number of days was used as a covariate, the difference between the lines became non-significant. Assuming linear growth in both lines and similar maintenance requirements per unit body weight, the authors concluded that "selection for postweaning gain caused a change in gross efficiency but not in net efficiency of tissue growth". This conclusion was unchanged in a subsequent study (Timon *et al.* 1970) of body composition and energetic efficiency in the lines. Whilst carcass energy per unit energy consumed was greater in the high than control line the authors suggest that this was due to increased intake in the high line.

Canolty and Koong (1976) found no difference in maintenance requirement but a substantially greater availability of metabolisable energy for gain in a line of mice selected for high weight gain than in a contemporaneous unselected control line. They concluded that selection for rapid postweaning gain did not alter the lean energy deposition coefficient which they defined as the proportion of available ME used for protein deposition multiplied by the net efficiency of ME utilisation for protein deposition, but did alter the fat energy deposition coefficient. The ratio of fat energy to protein energy deposition in their high and control lines was 2.3 and 1.1 respectively which would account for the significantly higher availability of ME in the high line.

One study with chickens which describes a departure from the general observation of a correlated improvement in gross efficiency with selection for increased weight gain was reported by Siegel and Wisman (1966). In that study they found that under *ad libitum* feeding their high weight and low weight lines had similar gross efficiencies when measured over an age constant period. Under restricted feeding, however, when high weight individuals were pair fed to their low weight counterparts, gross efficiency was greater in the high weight birds. From this the authors concluded that "changes in appetite could mask associated changes in feed utilisation unless the former is controlled". Since selection was for 8-week body weight and the birds in the study were tested over a growth period of from 1 to 4 weeks of age, the test period may in part account for the discrepancy with other reports. Studies by Lepore
(1965) and Proudman *et al.* (1970) with chickens have shown high weight lines to be more efficient than low weight lines on *ad libitum* feeding over age constant periods concluding at or near the age at selection.

A number of the above studies have included measures of body composition. Apart from these there are some separately reported studies of correlated response in body composition to selection for growth in mice (McPhee and Neill 1976, Brown *et al.* 1977, Biondini *et al.* 1968, Sutherland *et al.* 1974, Hayes and McCarthy 1976). Most reports have considered effects upon body composition at or near the age at selection. The majority of studies have shown high weight animals to be fatter at a given age than their low weight or control line counterparts. There have been a number of reported exceptions to this observation (Lang and Legates 1969, Fowler 1958, Biondini *et al.* 1968, Eisen *et al.* 1977) where certain lines of mice have showed no increase in fatness at a given age following selection for increased body weight gain. Fewer studies have looked at growth-related changes in fat deposition resulting from selection for increased growth rate. McPhee and Neill (1976) used this approach in their studies of body composition in lines of mice selected for high and low body weight. They found that high line mice became increasingly fatter with increasing body weight and concluded from differences between early and later generation responses that "selection for increased weight appeared to reduce the body weight at which fat was deposited at its maximum rate".

Some studies (e.g. Hull 1960, Hayes and McCarthy 1976) have shown age at selection to have a significant effect upon the growth-related pattern of fat deposition. Hayes and McCarthy selected mice for either high or low body weight at either 5 or 10 weeks of age. The high lines became progressively fatter than the low lines as growth proceeded and mice selected at the younger age for high weight were fatter than those selected at the older age. They concluded that although selection for high weight favours animals with large appetites no matter when selection is practised, at later ages screening will also occur for relatively lean animals, i.e. ones which grow more efficiently by depositing relatively less fat. Sather and Fredeen (1978) selected pigs on an index which combined increased growth rate with decreased back fat thickness. Such selection resulted in substantial genetic improvement in the two component traits and also a substantial improvement in feed efficiency.

Selection for growth under restricted feeding

There are a number of published reports of selection experiments with pigs and mice in which animals have been selected for increased growth rates on a quantitatively restricted intake (Fowler and Ensminger 1960, Falconer and Latyszewski 1952, Hetzel and Nicholas 1978, and McPhee *et al.* 1980). Fowler and Ensminger (1960) reported on nine generations of selection of pigs on an index which included number born, number weaned and rapid growth rate from weaning to 150 lb liveweight under either of two planes of nutrition. Feed efficiency was higher in the lines selected on the low plane of nutrition. There was a significant line by feeding level interaction from which the authors concluded that animals should be selected under the environment on which they are normally expected to be grown. Body composition data were not presented. The study of Falconer and Latyszewski (1952) appears to have been largely prompted as an experimental test of Hammond's thesis relating to the optimum selection environment. This is made apparent by the lack of
information on correlated response in food consumption/efficiency in the two lines. They did find, however, that growth rate was only marginally lower in restricted fed than in full fed line mice when tested on the *ad libitum* diet but that growth rate of full fed line mice was severely depressed under the restricted feeding regime. They further found that the restricted line mice were leaner than their full fed counterparts when both lines were reared on full feed.

Hetzel and Nicholas (1978) and McPhee *et al.* (1980) used mice to test the proposition that selection for increased weight gain with all animals receiving the same restricted amount of diet would favour those that were more efficient because they directed more ME towards protein and less towards fat synthesis. Hetzel and Nicholas found that the restricted fed line on *ad libitum* feed was leaner than its contemporaneous control at the same age and weight. The full fed line on *ad libitum* feed, whilst of similar fatness at a given body weight, was fatter at a given age. The improvement in body composition in the restricted line was, however, offset by an improvement in growth rate of only one quarter, and in gross efficiency and lean tissue food conversion of only one half that obtained with selection on full feeding. McPhee *et al.* (1980) found that their two lines selected under restricted feed were faster than the control line whether measured at the same age or body weight. On *ad lib* feeding selection increased food intake per unit time by 6% and gross efficiency by 12%. They concluded that the increased growth and energy retention in the restricted fed lines was brought about most likely by a reduction in the maintenance requirement. Unfortunately they did not run a contemporaneous line selected for weight gain under *ad libitum* feeding so that such comparison was not possible.

Selection for increased growth rate where all animals are restricted to the same level of intake on a daily basis, depending upon the level of restriction, may favour animals with small absolute maintenance requirements but with also relatively small growth potential. Since maintenance accounts for a relatively large proportion of ME intake and since maintenance requirements must be met before energy is available for growth, a moderate reduction in ME intake means a large reduction in ME available for growth. Thus where all animals regardless of initial size or growth potential are allocated a set restricted amount of diet, larger animals even with a higher maintenance efficiency (i.e. per unit live weight or per unit metabolic weight) will be penalised since considerably less dietary energy will be available for growth. It should be noted, however, that McPhee *et al.* (1980) preselected animals by omitting extremes of both high and low body weight at commencement of test and the selection criterion used was weight gain adjusted by linear regression to the average 5-week weight of each line x sex class.

Selection for feed efficiency

There have been a number of reports of selection for feed efficiency *per se* in chickens, pigs, rats and mice.

**Chickens**

Wilson (1969) provided information from one generation of selection for increased 5 to 10-week weight gain and decreased FCR (*feed/gain*) in chickens. He obtained an average realised genetic correlation of -0.51 between gain and...
FCR and calculated that selection for gain would reduce the amount of feed needed to produce one unit of gain about 75% as much as direct selection for feed efficiency. He discussed the concept of metabolic efficiency which was defined as the efficiency of an individual metabolic system in converting feed energy into body tissue and was measured by variation in gain independent of food consumption and initial weight. The heritability estimate of metabolic efficiency was about 0.4 which was similar to the estimate for gross efficiency. Wilson suggested that variation in gross efficiency is primarily the result of differences in metabolic efficiency.

In a study of feed efficiency and its relationship with body weight in chickens, Guill and Washburn (1974) selected three broiler lines and one previously random bred population for either high or low FCR each with body weight either unrestrained or held constant. The broiler lines were selected for three generations and the random bred derived population for one generation. It is significant to note that in the lines selected for low FCR there was virtually no difference in response between the body weight constant and the body weight varied lines in both the random bred population and the broiler lines. The realised heritability of FCR was similar, within the same class of stock, for the body weight constant and varied lines whereas the overall heritability for FCR was higher (0.42) in the random bred population than the average of the three broiler lines (0.25). They concluded that even in lines previously selected for growth there is sufficient variation in efficiency of feed utilisation to allow progress in selection without further change in body weight. In neither of the above studies were measurements made of body composition.

More recently Pym and Nicholls (1979) presented details of a selection experiment in chickens in which birds were selected for either increased weight gain (line W) increased food consumption (line F) or decreased FCR (feed/gain, line E) over a test period of 5 to 9 weeks of age. An unselected control (line C) was also maintained. Realised heritability estimates calculated after 10 generations of selection were: gain (G) 0.30, food intake (F) 0.36 and FCR 0.26 whilst realised generation correlations were: G:F +0.64; G:FCR -0.50 and F:FCR +0.22. The latter correlation has little relevance since there was large asymmetry in the correlation, i.e. selection for decreased FCR had no effect upon food consumption whereas selection for increased food consumption resulted in a substantial increase in FCR.

Body composition analyses (Pym and Solvyns 1979) showed selection for increased food consumption (line F) to result in a considerable increase in body fat whereas selection for improved feed efficiency (line E) resulted in a significant reduction in body fat whether measured at a given age or weight. Selection for gain (line W), however, had no effect upon body composition whether measured at a given age or weight. In a study of energy metabolism in the four lines at generation 3 (Pym and Farrell 1977) there was no difference between lines in the availability of ME for growth but there were differences in maintenance energy requirements in which the E line was lowest (796 kJ/kg w/d), the F line highest (937 kJ/kg w/d) and the W and C lines similar and intermediate. In a recent study of the lines at generation 10, metabolisability of dietary energy was calculated to be 75.4 ± 0.7%; 73.8±0.7%, 77.0 ± 1.04% and 76.0 ± 0.7% in the W, F, E and C lines respectively.
These results indicate that selection for increased weight gain has improved gross efficiency almost entirely as a result of the correlated increase in food consumption leading to a reduction in the proportion of intake used for maintenance. Since there was no similar increase in intake in the line selected for improved food conversion efficiency, this does not account for any of the observed improvement in efficiency in this line. Such improvement is probably largely attributable to the lower energy in the tissue deposited and to a lesser extent to a marginally higher metabolisability of dietary energy and lower maintenance energy requirement in this line. On the other side of the coin, the substantial increase in FCR, i.e. depression in gross efficiency observed in the line selected for increased food consumption is due to a large increase in the deposition of body fat, an increase in the maintenance requirement and a decrease in the metabolisability of dietary energy. These factors together appear to have swamped any beneficial effect of increased food consumption resulting in a spreading of the maintenance requirement.

It has been stated that selection for increased growth rate at early physiological ages is essentially the same as selection for increased appetite. The large differences in response in the W and F lines in this experiment show this patently not to be the case.

Pigs

Dickenson and Grimes (1947) selected pigs for high or low food requirements from weaning to constant weight for five generations. After five generations of selection food requirement was reduced by 5.2% in the efficient line and increased by 6.6% in the inefficient line. The realised heritability of FCR was calculated at 0.24 and the genetic correlation between FCR and daily gain was -0.78. On the basis of this they suggested that selection based on rate of gain from weaning to market weight should be nearly as effective in improving efficiency as direct selection for efficiency. Body composition was not measured in their study. Bernard and Fahmy (1970) conducted a selection experiment with pigs for ten generations in which animals were selected either for improved feed efficiency (E), increased carcass score (S) or on an index combining these two traits (ES) over a weight constant interval from 23 to 90 kg. Carcass score included carcass length, back fat thickness, loin eye area and belly grade in which the maximum possible score was 100. Selection in all lines improved feed efficiency and carcass score. Heritability estimates for FCR and carcass score were 0.16 and 0.43 respectively and the realised genetic correlation between the traits was -0.52. Feed requirement was reduced by 0.09 and 0.24 kg/year in the E and ES lines respectively whilst carcass score was increased by 0.77 and 0.97 in the S and ES lines respectively. They explained the greater response in the two traits in the index line than in the single trait lines as being due to a larger selection differential in this line and the positive genetic correlation between the traits. Whilst the relative contribution of leaness to carcass score was not defined, the results indicate a positive association between feed efficiency and leaness in pigs. Jungst et al. (1981) presented data from a study of five generations of selection for improved feed efficiency in Yorkshire pigs measured over a weight constant interval from about 23 to 100 kg. The realised heritability of feed/gain calculated after 5 generations of selection was only 0.09. Correlated responses in rate of gain, daily food consumption and back fat thickness were
all small and the regression coefficients non-significant. The authors concluded that response to direct selection for feed efficiency in pigs may not be sufficiently great to warrant the time and money required to measure individual food consumption.

**Rats**

Morris et al. (1933) reported a selection experiment in which rats were selected for either high or low feed efficiency. Animals in the two lines were all descended from a single pair mating. The low efficiency line was about 40% less efficient than the high efficiency line after seven generations of selection. A study of body composition in the lines (Palmer et al. 1946) revealed that the high efficiency strain not only started the test period with a higher proportion of fat in their carcasses but that the difference in fatness became greater as the animals matured.

**Mice**

The earliest study of selection for feed efficiency in mice was reported by Sutherland et al. (1970) and the body composition comparisons by Biondini et al. (1970). They selected for increased weight gain from 4 to 11 weeks of age in three replicate lines for 9 generations. Thereafter one replicate line continued to be selected for increased weight gain (G), a second was selected for increased food consumption (F) and the third for improved feed efficiency (E) (gain/food). In the first 9 generations of selection there were marked increases in gain, moderate increases in food intake and marked increases in gross efficiency. After the introduction of the new selection criteria rate of gain and feed intake continued to increase in all three lines, while gross efficiency similarly improved.

Realised heritabilities calculated in generation 10 to 21 for gross efficiency and food intake were 0.17 and 0.20 respectively and genetic correlations among the three traits pooled over generations were: G:F + 0.88, G:E + 0.91 and E:F + 0.52. Body composition comparisons showed significant differences in percent fat in the three replicate lines selected for weight gain at generation 9 prior to the change in selection criteria. The line subsequently selected for increased food consumption was somewhat lighter but considerably leaner than the other two lines. Unfortunately since there were obvious significant genetic differences between the three replicate selected lines prior to the change in selection criteria, it is not possible to assess the effects of the subsequent selection free of this bias. Notwithstanding this, the results provide an indication of the likely directional effects of such selection if not an accurate estimate of their relative effects in the one population. Following the change in selection criteria, there was a slight increase in fatness in the efficiency line, a moderate increase in the gain line and a substantial increase in the line selected for increased intake. After five generations of selection for improved gross efficiency, the efficiency line was still almost twice as fat as the control line.

Eisen (1977) described an experiment in which mice were selected for feed efficiency using a restricted selection index where the goal was to maximise genetic change in postweaning weight gain from 3 to 6 weeks of age whilst keeping genetic response in feed intake to zero. He obtained realised
heritabilities after ten generations of selection of the order of 0.2 and a pooled realised genetic correlation between feed intake and post weaning gain of +0.36. The major objective of the study, namely to change feed efficiency whilst holding genetic change in feed intake at zero was obtained up to one standard deviation from the mean of postweaning gain. Outside this range the genetic correlation between post weaning gain and feed intake was altered sufficiently to invalidate the selection index. Body composition was not measured. It is interesting to note that the predicted and observed responses in the increased efficiency line in this study are essentially similar to those predicted by Pym and James (1979) for an economic index optimising response with respect to body weight and food consumption in chickens, viz., maximising response in gain but effectively restricting response in food consumption to zero. Because of the particular economic weightings to feed and liveweight in broiler production, it would appear that a restricted index could be used to good effect in broiler breeding programmes.

Yüksel et al. (1981) presented data from a selection experiment in which mice were selected for improved feed efficiency (gain/feed) on either an ad libitum or restricted feeding regime at either of two ages. They found relatively low realised heritability estimates of 0.13 for feed efficiency. There were no interactions for liveweight, weight gain or feed efficiency between line and feeding regime, i.e. selection under fixed intake led to the same increase in appetite as did that under ad libitum feeding. They considered this to be an unexpected result and drew comparisons with the results of Hetzel and Nicholas (1978) who had selected for gain under ad libitum and restricted feeding regimes. Whilst they acknowledged this difference in selection criteria it is worth noting that the equivalent comparison in the chicken study of Pym and Nicholls (1979) would be between the E and the W lines. There are major differences in appetite, body composition and energy metabolism between these two lines which could be readily seen as contributing to differential response to restricted feeding. Their study showed no interactions for carcass composition and selection for efficiency led to an increase in fatness on both selection regimes and both age ranges.

Gunseth et al. (1981) presented data from a selection experiment in mice in which two lines were selected for 4 generations for efficiency; one for maximum gain from initial weight until they consumed 100 g of feed (FF) and the second was for efficiency over a weight constant period (FG). They used the method of Parks (1970) for predicting the 'true' efficiency of growth, i.e. free of maintenance. Parks' methods assume that body weight is a function of both age and feed intake. Similar and significant gains in liveweight were made in the two selected lines and realised heritability for FF was 0.56 and for FG was 0.73 and the genetic correlation between them was -0.94. The results indicated that either method of selection would be effective in changing gross efficiency. However, using Parks' techniques the results indicated that selection for gross efficiency did not improve their ability to incorporate feed into biomass; all three lines had essentially identical values for this parameter. They suggested that gross efficiency was changed by reduction in the maintenance component. They did not report on body composition analyses.

**SPECIES COMPARISONS**

Laboratory species have been used in selection experiments for many years.
as models for the larger livestock species because of the very great reduction in costs and time involved in obtaining meaningful comparisons from a reasonable number of generations of selection. In most instances the physiological factors contributing to responses in the two systems have been reasonably equatable. It is, however, somewhat perturbing that where mice and rats have been selected for some measure of feed efficiency, where body composition measurements have been taken, such animals are frequently found to be fatter than their unselected counterparts (e.g. Palmer et al. 1946, Dickerson and Gowen 1947, Biondini et al. 1970, McPhee et al. 1980, and Yüksel et al. 1981). This disagrees with most of the equivalent studies in the larger species and with expectations based upon the energy cost of depositing muscle and fat in the body.

As pointed out by Webster (1977) some 70% of a growing animals energetic input is dissipated as heat and that protein synthesis associated with the high turnover rate of protein in the body, accounts for a significant proportion of this heat output. Yüksel et al. (1981) in explaining their results, have suggested that the differential demands of laying down fat and lean may account for perhaps a small part of the total energetic input and that "the alternative outlets" may have swamped the system.

It is nonetheless true that mice are small animals with relatively poor food conversion efficiency stemming from a high energetic requirement for thermoregulation associated with their large surface area to weight ratio. Animals with relatively large subcutaneous deposits of fat would be undoubtedly better insulated to heat loss than their leaner counterparts and would thus require less food to maintain body heat. In larger animals thermoregulation is relatively of lesser importance and partitioning of protein and fat within the body would have a greater relative influence upon food utilisation efficiency. Whilst chickens are much smaller than pigs and cattle their feathers provide a very effective insulation to heat loss. To test whether this factor is important in explaining the apparently anomalous finding in small laboratory animals, selection could be practised for feed efficiency under a number of different temperature environments. This is not to suggest that laboratory animal studies in this area have been of questionable value but rather to pose a cautionary note to unqualified extrapolation to the larger species.

CONCLUSIONS

This review provides ample evidence that the genetic and physiological interrelationships between growth, feed efficiency and body composition are very complex. Whilst most published information in this area has contributed to a greater understanding of the factors involved, considerably more detailed experimental information is yet required before breeders can formulate effective breeding programmes which optimise economic response in the component traits.

SUMMARY

The paper reviews the literature on selection experiments in intensive livestock species and laboratory animals in which food utilisation efficiency for growth has been either a trait under selection or measured as a correlated trait to selection for growth. Several different methods of expressing food utilisation efficiency are described and the component factors contributing to genetic change in gross efficiency are considered.
The genetic and physiological relationships between growth, efficiency and body composition are shown to be complex. Notwithstanding the large body of data already available, breeders require additional experimental information in each species to enable formulation of effective breeding programmes which optimise economic response in these traits.

КРАТКОЕ СОДЕРЖАНИЕ

В этой статье представлен обзор литературы по селекционным опытам в области интенсивных видов скота и лабораторных животных, в которых эффективность использования пищи для роста является или признаком при селекции или измеряется как корреляционный признак для селекции роста. В статье освещаются несколько различных методов выражения эффективности использования пищи, а также рассматриваются составные части, способствующие генетическому изменению эффективности роста.

Генетическая и физиологическая взаимосвязь между эффективностью, ростом и составом организма представляет собой сложный. Несмотря на значительное количество опытных данных в настоящее время, селекционеры всё ещё нуждаются в дополнительной экспериментальной информации по отдельным видам, чтобы иметь возможность составить эффективные программы разведения пород, имеющих оптимальное экономическое решение в этих характеристиках.

REFERENCES